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Typical cyperoid reproductive structures in *Lipocarpha humboldtiana* and *Ascolepis brasiliensis* (Cypereae – Cyperoideae – Cyperaceae): New evidence from a development perspective

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ABSTRACT

Ascolepis and *Lipocarpha*, Cyperaceae, have highly reduced reproductive structures and hypogynous scales that are controversially appreciated. Because of this, flowers and spikelets and, thus, inflorescences have been interpreted in different ways, which, in turn, has led to placing the two genera in different tribes. Some authors interpret spikelets in *Ascolepis* and *Lipocarpha* as many-flowered and the so-called hypogynous scales as homologous to the lateral scales of *Hypolytrum*, or consider these scales comparable to a *Scirpus* bristle. However, many other authors consider spikelets in *Lipocarpha* and *Ascolepis* to be a result of a reductional process from a many-flowered cyperoid spikelet to a single-flowered spikelet, where the adaxial and abaxial hypogynous scales may be seen as the respective prophyll and glume of the reduced spikelets. The latest molecular phylogenies of Cyperaceae show both genera nested in the *Cyperus* clade, forming, in turn, a clade together with the rest of the Cypereae genera having single-flowered spikelets and hypogynous scales. Alternatively, based on this, the scales of uncertain homology that accompany the *Ascolepis* and *Lipocarpha* flower might be seen as special reproductive formations, representing a synapomorphy of such clade, instead of relicts of an ancestor with many-flowered spikelets. In view of this, freshly collected inflorescences of *Lipocarpha humboldtiana* Nees and *Ascolepis brasiliensis* (Kunth) Benth. ex C. B. Clarke were studied using light and scanning electron microscopy, with the aim of elucidating the nature of the controversially interpreted reproductive structures of these species from a development perspective. Results show that the "hypogynous scales" simply represent vestigial structures derived from the reduction of typical cyperoid spikelets, rather than a perianth part or specialized formations emerging as evolutionary novelties. Two scales are typically generated in both species, one being abaxial and the other adaxial, homologous to a glume and a prophyll, respectively, which contrasts with the ephrophyllate condition so far attributed to *Ascolepis*. In both cases, the inflorescence is a spike of reduced spikelets, and the floral development in *L. humboldtiana* and in *A. brasiliensis* follows the general ontogenetic pattern observed in Cyperoideae. These characteristics support the inclusion of both genera in the Cypereae tribe.

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Introduction

The relatively recent development of molecular phylogenies is revealing that generalizations in the interpretation of complex plant structures often obscure variation and developmental patterns important for understanding the evolution of forms (Pozner et al., 2012). In Cyperaceae, understanding the structure and homologies of inflorescences is one of the main concerns among cyperologists (Kukkonen, 1994; Raynal, 1971), because the inflorescence has proved to be a source of reliable diagnostic traits, indicating phylogenetic pathways (Bruhl, 1995; Goetghebeur, 1998; Guarise and Vegetti, 2007, 2008; Tucker and Grimes, 1999). Within Cyperaceae, the basic reproductive units are the spikelets (Richards et al., 2006; Richards, 2002; Vrijdaghs, 2006), which bear highly simplified flowers and are arranged in usually complex and congested inflorescences (Goetghebeur, 1998; Reutemann et al., 2012; Vegetti, 2003). The structure of spikelets and inflorescences within the family is a controversial topic that has been interpreted in varying ways, which has consequently led to frequent taxonomic disagreements (Muasya et al., 1998).

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In *Ascolepis* Nees ex Steud. (about 20 spp.) and *Lipocarpha* R. Br. (about 35 spp.), the inflorescence is currently interpreted as a head of one to few spikes made up by many single-flowered spikelets, which are eprophyllate and with one single glume in *Ascolepis* (Goetghebeur, 1980, 1998), whereas they may have either a glume or a prophyll in *Lipocarpha*, or show a partial or complete reduction of either the single glume or the glume and the prophyll (Goetghebeur and Van den Borre, 1989). Such extremely reduced condition of the spikelets, with one single bisexual flower, and generally one or two "hypogynous scales", has led to ambiguous interpretations of the reproductive structures in both genera.

Due to disagreements in the interpretation of flowers, spikelets and inflorescences in *Ascolepis* and *Lipocarpha*, different authors have placed these genera in different tribes. Kunth (1837), Nees von Esenbeck (1842) and Pax (1886) interpreted the inflorescence of *Ascolepis* and *Lipocarpha* as a head of one or few many-flowered spikelets, with the glumes placed spirally, and the hypogynous scales were thought to be homologous to the scales observed in *Hypolytrum* Pers. species. Clarke (1901) and Kern (1974) also interpreted the inflorescence in both genera as a head of many-flowered spikelets, with a bisexual flower in the axil of each glume, and the hypogynous scales were considered homologous to the *Scirpus* L. bristles. Another interpretation of the inflorescence in *Ascolepis* and *Lipocarpha* was made by Eiten (1976), who considered the spikelet in both genera as reduced to a short rachilla and a single lateral flower. In this context, Holm (1899) suggested that a reductional process from a many-flowered spikelet to a single-flowered spikelet takes place in *Lipocarpha*, where the adaxial and abaxial hypogynous scales might be seen as the prophyll and the glume of the reduced spikelets, respectively, and almost the same pattern may be recognized in *Ascolepis*, although there is no prophyll (Goetghebeur, 1977). Consequently, depending on how the reproductive structures were understood in *Ascolepis* and *Lipocarpha*, these genera got to be included within the Hypolytreae, Scirpeae or Cypereae tribes.

The location of *Ascolepis* and *Lipocarpha* in the Cypereae tribe based on the spikelet structure is currently supported by molecular phylogenies of the Cyperaceae family, where *Ascolepis* and *Lipocarpha* are embedded in the *Cyperus* clade (Muasya et al., 1998, 2000, 2009a,b). Although inflorescences with single-flowered spikelets and hypogynous scales are rare within Cypereae, both structures characterize exclusively the *Alinula* J. Raynal, *Ascolepis*, *Lipocarpha* and *Volkiella* Merxm. & Czech genera, which, with the exception of *Alinula*, are nested at the level of one single node in the most recent phylogenetic hypothesis for the Cyperaceae family (Muasya et al., 2009a). Alternatively, based on these data, the scales of uncertain homology that accompany the *Ascolepis* and *Lipocarpha* flower might be seen as special reproductive formations, representing a synapomorphy of the *Ascolepis*-*Lipocarpha*-*Volkiella* clade, instead of relicts of an ancestor with many-flowered spikelets.

Numerous studies on the structure and development of flowers and spikelets in species with many-flowered spikelets have been carried out in the family (Blaser, 1941, 1944; Bruhl, 1991, 1995; Celakovský, 1887; Eiten, 1976; Gehrke et al., 2012; Goetghebeur, 1986, 1998; Haines and Lye, 1976; Holttum, 1948; Kern, 1962; Kukkonen, 1986; Mattfeld, 1938; Meert and Goetghebeur, 1979; Meeuse, 1975; Mora-Osejo, 1960, 1987; Muasya, 1998; Nijalingappa and Goetghebeur, 1989; Pax, 1886; Payer, 1857; Raynal, 1971; Reynders et al., 2012; Richards et al., 2006; Richards, 2002; Schönland, 1922; Timonen, 1998; Vrijdaghs et al., 2004, 2005a,b,c, 2006, 2007, 2009, 2010, 2011; Zhang et al., 2004a,b). These papers frequently discuss the euanthial and pseudanthial hypotheses and the monopodial or sympodial interpretation. However, such studies are rare on species with single-flowered spikelets. In view of this, in this study, we intend to clarify the nature of the so-called hypogynous scale in two tropical to subtropical herbs, *L. humboldtiana* Nees and *A. brasiliensis* (Kunth) Benth. ex C.B. Clarke, from a development perspective and, building on it, define the structure of the spikelet and the inflorescence in both species.

Materials and methods

The material examined was collected in Misiones, Argentina. Vouchers are deposited at Herbario Arturo Ragonese (SF). Material collected of *L. humboldtiana*: Guarise 258, 280, 295. Material collected of *A. brasiliensis*: Guarise 257; Guarise and Reinheimer, 396.

Fresh inflorescences of *A. brasiliensis* and *L. humboldtiana*, covering developmental stages from the earliest ones up to the differentiation of stamens and carpels, were fixed in FAA (formalin:acetic acid:70% ethanol, 10:5:85, v/v). For SEM observation, fixed inflorescences were dissected and classified using a stereoscopic microscope according to their different stages of development. The samples were dehydrated through a graded ethanol series plus two final changes of 100% acetone. The dehydrated material was critical point dried with CO_2 as transitional fluid and coated with gold-palladium. All samples of inflorescences, spikelets and flowers were observed and photographed using a PHILIPS XL 30 scanning electron microscope from the Electron Microscopy Service of the Bernardino Rivadavia Museum, Buenos Aires.

For the light microscopy study, inflorescence primordia were fixed in FAA for 48 h, washed in distilled water and transferred to 5% hydrofluoric acid for 24 h to remove silica (Metcalfe, 1971). Then, the material was rinsed in distilled water, dehydrated through a graded ethanol series and embedded in paraffin following the protocol proposed by D'Ambrogio de Argüeso (1986). From the embedded material, longitudinal sections were cut 5–10 μm thick using a rotary microtome and stained with safranin, fast green and Mayer's haematoxylin (Johansen, 1940). Lastly, the samples were mounted in Canada balsam, examined under a Mikoba S-800 microscope and photographed using a Canon Power Shot A640 digital camera.

Results

Morphology of the mature inflorescence

The adult inflorescence of both species is capitate, with one terminal and few to several laterals spikelet-like spikes in *L. humboldtiana* (Fig. 1A and B), and only one terminal or a terminal plus few lateral spikelet-like spikes in *A. brasiliensis* (Fig. 1C and D). The lateral spikes are complex first and second order axes in *L. humboldtiana*, and only complex first order axes in *A. brasiliensis*. Each spike is truncate, i.e., lacks terminal spikelet, and bears lateral single-flowered spikelets spirally arranged (Fig. 1B and D). These lateral spikelets are normal branches emerging from a bract axil.

Inflorescence development

Development of the *L. humboldtiana* inflorescence starts with the production of bracts and first-order lateral axes primordia, spirally arranged and in acropetal succession (Fig. 2A). While the proximal first-order lateral axes begin differentiating as complex lateral axes, the inflorescence apical meristem starts forming distal primary spikelet primordia, which will together become the inflorescence terminal spike (Fig. 2B). Below the terminal spike, each complex first-order lateral axis may: (1) produce a variable number of complex second order axes (which carry third-order spikelets), and then produce second-order spikelets that will form

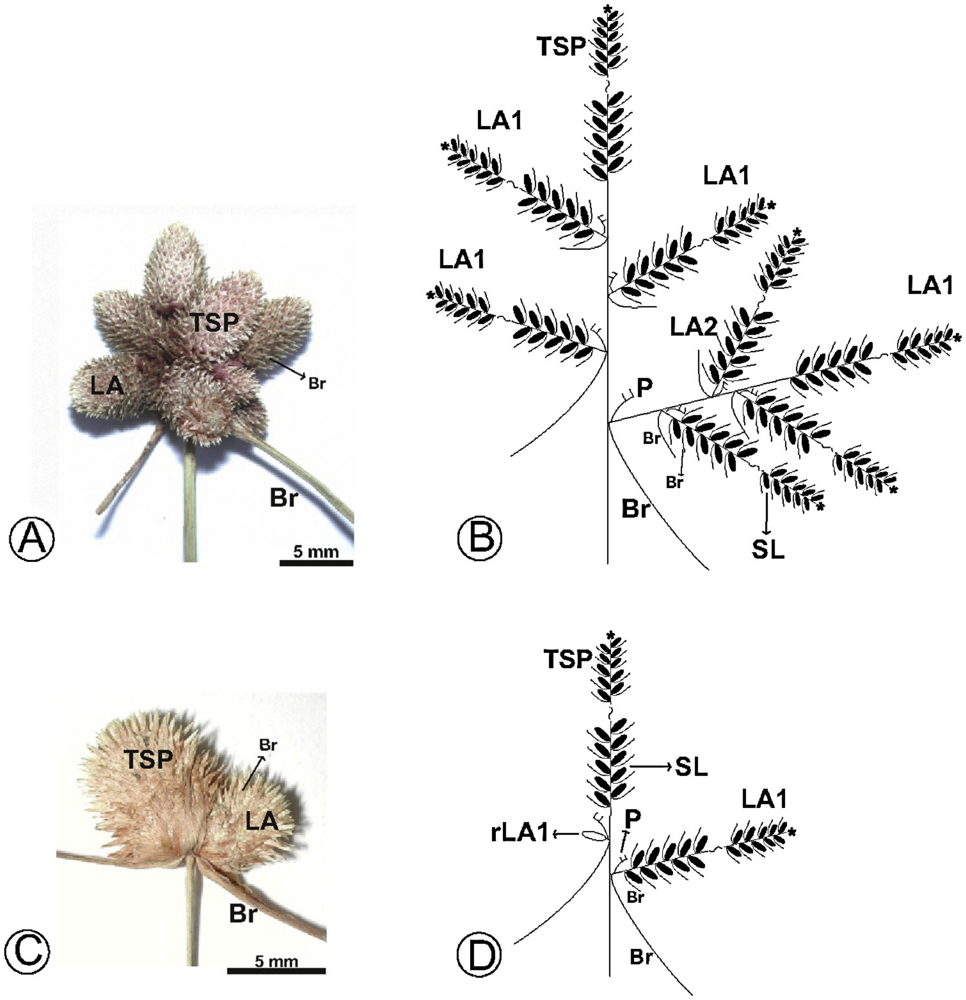

Fig. 1. Morphology of the mature inflorescence in *Lipocarpha humboldtiana* and *Ascolepis brasiliensis*. (A) General appearance of the inflorescence in *L. humboldtiana*. (B) Inflorescence structure in *L. humboldtiana*. (C) General appearance of the inflorescence in *A. brasiliensis*. (D) Inflorescence structure in *A. brasiliensis*. *Abbreviations*: Br, bract; LA, complex lateral axis; LA1, complex lateral axis of first order; LA2, complex lateral axis of second order; rLA1, reduced lateral axis of first order; P, prophyll; SL, spikelet; TSP, terminal spike. The asterisks in (B) and (D) indicate the absence of the terminal spikelet.

the terminal spike on the first-order axis or (2) only develop the terminal spike on the first-order axis (Fig. 2C). The inflorescence terminal spike grows to a larger extent and its spikelets differentiate earlier than those in the lateral spikes (Fig. 2B and C). Inflorescence development in *A. brasiliensis* is similar to that observed in *L. humboldtiana*, but with less or even no development of the so-called lateral spikes (Fig. 2D).

Spikelet development

In both species, primary, secondary and sometimes tertiary spikelet primordia, located in the axil of glume-like bracts, begin their differentiation by generating a prophyll, which emerges as two lateral bulges overgrown by the spikelet primordium (Figs. 3A and 4A). These lateral bulges correspond to the two keels which are observed in the mature prophyll. While the prophyll starts differentiating on the adaxial face of the developing spikelet, a glume and then a flower primordium initiate in an opposite position to the prophyll (Figs. 3B and 4B). During the differentiation of the flower primordium, the two species show differences in terms of the relative development of the glume and the prophyll, and also in how much each of these phyllomes finally contributes to protecting the flower. In *L. humboldtiana*, the prophyll continues growing on its adaxial face and the keels (Fig. 3C and D), and then on the adaxial and abaxial faces, with the keel margins completely covering the developing glume and flower (Fig. 3F and G). When the glume is at an advanced stage of development, it grows to cover most of the flower (Figs. 3I and 5A). By comparison, in *A. brasiliensis*, the prophyll stops growing at this time (Figs. 4B–D and 6A,B) and may no longer be observed at advanced stages of development (Figs. 4E,F and 6C). On the abaxial face of the flower primordium, the glume becomes differentiated, expanding first laterally and then on the margins and the apex, and completely enveloping the developing flower (Fig. 4C–F). The margins of the glume do not fuse together, but develop to a great extent, enveloping the adaxial and abaxial faces of the developing flower (Figs. 4F and 5B). Only in *A. brasiliensis* during the early developmental stages of the glume and the flower, the apical spikelet meristem may be observed (Fig. 4D–F), which stops growing at early stages, with its sterile tip appearing adaxially due to the displacement caused by the development of the floral primordium (Fig. 4G). Because of this, the floral primordium first and then the flower have a pseudo-terminal position (Fig. 4D–I).

Flower development

The floral primordium expands laterally in the axil of the developing glume in both species, forming in *L. humboldtiana* two lateral

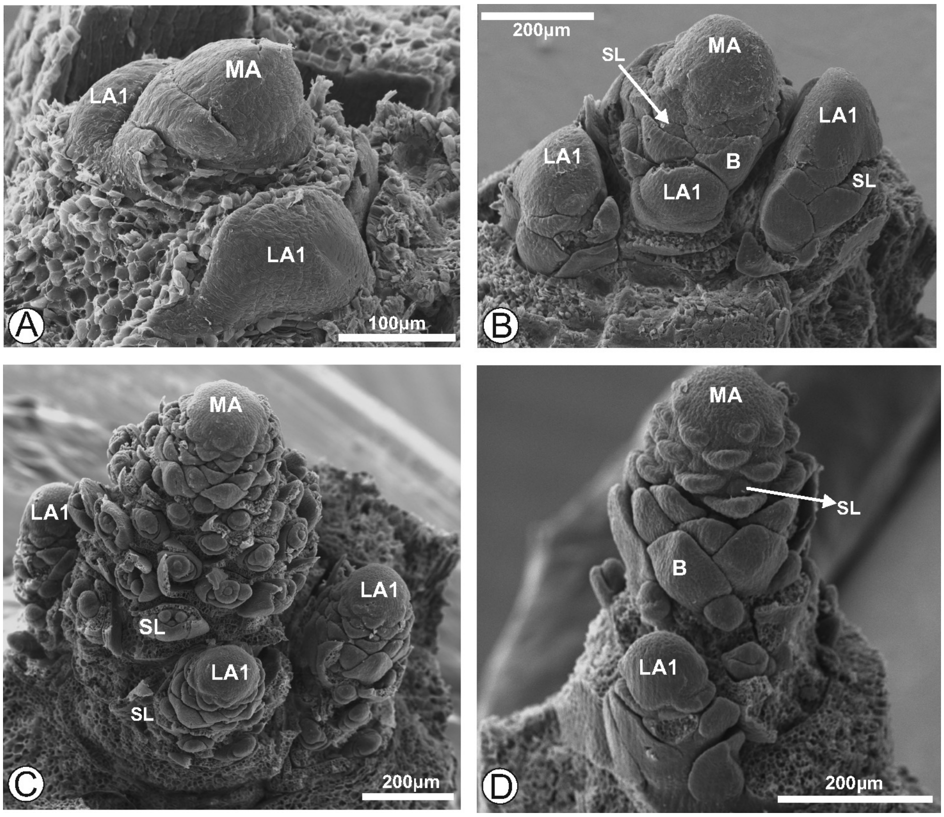

Fig. 2. Inflorescence development in *Lipocarpha humboldtiana* and *Ascolepis brasiliensis*. (A–C) *L. humboldtiana*. (D) *A. brasiliensis*. Abbreviations: B, bract; LA1, complex lateral axis of first order; MA, main axis of the inflorescence; SL, spikelet.

stamen primordia (Fig. 3C), followed by the formation of a third, abaxial stamen primordium (Fig. 3D) which, unlike the other two, does not develop (Fig. 3E). In this species the lateral primordia may both become functional stamens; alternatively one of them or even both may abort at later developmental stages, the latter leading to a female flower (Figs. 3H–J and 5A). In contrast, only one lateral stamen is formed in *A. brasiliensis* (Figs. 4C and 5B). After the initiation of stamens, the floral apex swells and then forms two primordia in both species, an annular ovary primordium (with three in *L. humboldtiana*, or two in *A. brasiliensis*, congenitally fused carpel primordia forming its wall) surrounding a central ovule primordium (Figs. 3D and 4C,D). Subsequently, the ovary primordium grows up from the base enveloping the central ovule (Figs. 3E and 4E) and, on the top of the ovary wall (three in *L. humboldtiana* or two in *A. brasiliensis*) stigma primordia originate (Figs. 3F–H and 4F,G). The median stigmatic branch is smaller than the lateral ones in *L. humboldtiana*, and this one is the one that is lacking in *A. brasiliensis*. At a later stage, a single style without a style base is formed in both species (Figs. 3J and 4H,I).

In no case any tepal primordia differentiate, and the abaxial (glume) and the adaxial (prophyll) scales are clearly distinct from a stamen and a carpel primordium (Figs. 3 and 4).

Discussion

Present developmental studies suggest that, both in *A. brasiliensis* and *L. humboldtiana*, the hypogynous scales simply represent vestigial structures derived from the reduction of typical cyperoid spikelets. This is consistent with what Holm (1899) proposed for *Lipocarpha*, and Goetghebeur (1977) for *Ascolepis*, based on the study of adult structures. Hypogynous scales do not either constitute perianths parts, nor specialized structures that might emerge as evolutionary novelties within the *Ascolepis-Lipocarpha-Volkiella* clade (Muasya et al., 2009a).

In both species, two scales are typically generated, one being abaxial and the other adaxial, homologous to a glume and a prophyll, respectively. The presence of a prophyll as recognized in *A. brasiliensis* contrasts with the eprophyllate condition so far attributed to the spikelets of the *Ascolepis* genus (Goetghebeur, 1980, 1998). Both in *L. humboldtiana* and in *A. brasiliensis*, the prophyll develops in a similar fashion to that described by Guarise et al. (2012) in the *Cyperus* L. species, although in *A. brasiliensis* the prophyll stops developing at an early stage and may no longer be observed during subsequent development stages or in the adult spikelet. The different development of the glume and the prophyll in *A. brasiliensis* and *L. humboldtiana* determines the formation of non-homologous foliar utriculiform structures protecting the flower, made up by the prophyll and the glume in *L. humboldtiana*, and only by the glume in *A. brasiliensis*. In the latter, the margins of the glume do not fuse together, unlike what had been interpreted by Kunth (1837), Nees von Esenbeck (1842), Pax (1886) and Barros (1938).

In genera of the *Cyperus* clade, the many-flowered spikelet consists of an indeterminate rachilla and distichously arranged glumes of acropetal development, each subtending (or not) a bisexual (or unisexual) flower (Eiten, 1976; Goetghebeur, 1998; Kukkonen, 1994; Vrijdaghs et al., 2009, 2010). The reduced spikelets of Cypereae with one single flower differentiate into two groups: those having a rachilla extension present, and those lacking a rachilla remnant. The presence of such rachilla remnant in *A. brasiliensis* is evidence of the monopodial branching of its spikelets, while the absence of such a structure in *L. humboldtiana*, possibly due to the extreme reduction of its spikelets, makes the interpretation of the branching type in this species more challenging.

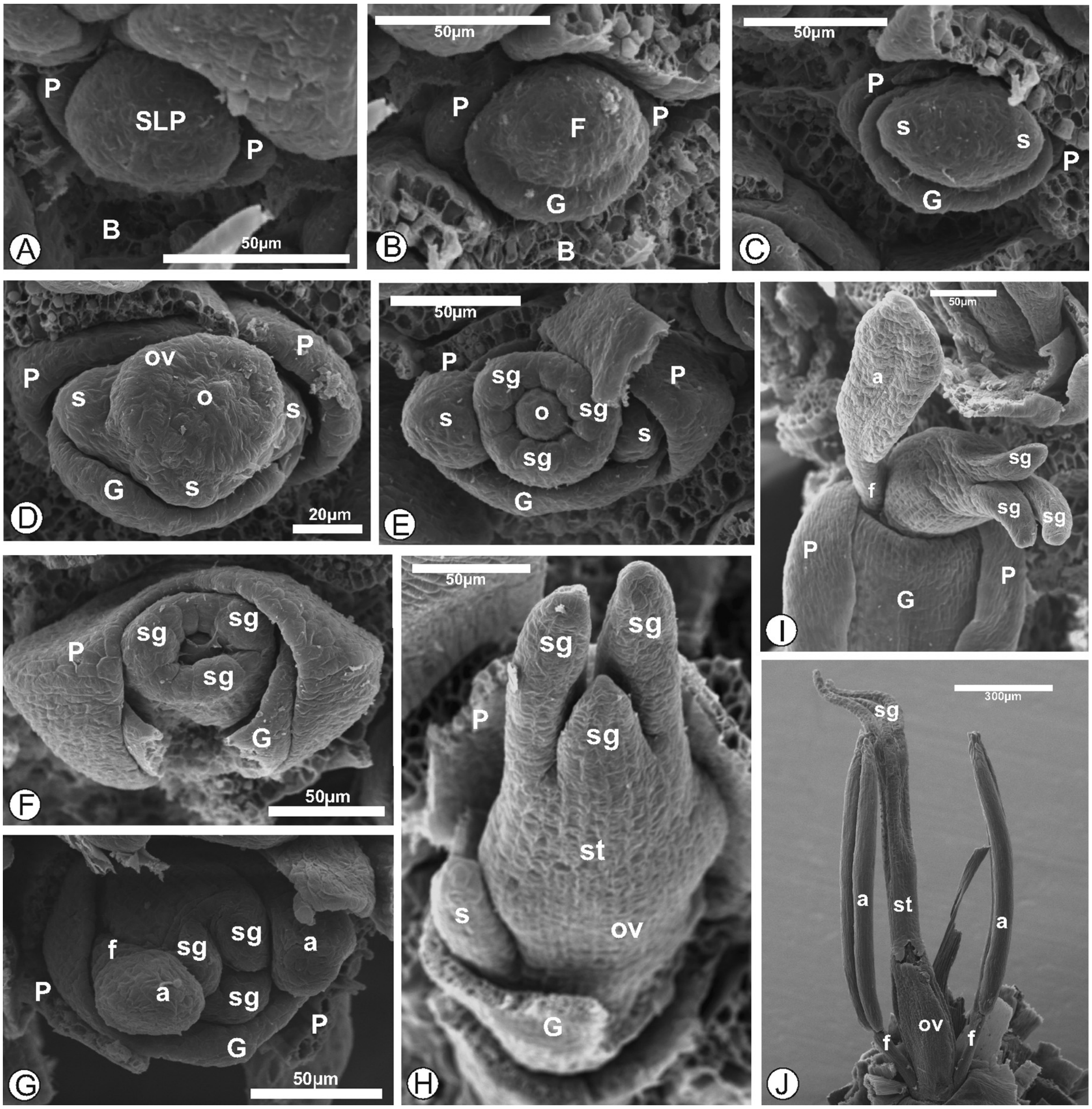

Fig. 3. Spikelet and floral ontogeny in *Lipocarpha humboldtiana.* (A) Development of the primordium of the spikelet and the prophyll in the bract axil. (B) Apical view of the spikelet, the glume primordium differentiating opposite the prophyll. Note the bi-keeled nature of the prophyll (C) In the floral meristem, the two lateral stamen primordia differentiate. (D) Emergence of the gynoecium primordium in the central part of the floral meristem, with the differentiation of the outer ovary wall and the central ovule. Note the emergence of the third stamen primordium on the adaxial part of the gynoecium primordium. (E) Differentiation of three stigma primordia on the ovary wall. Note that the lateral stamen on the left develops to a larger degree than the lateral stamen on the right while the third, abaxial stamen is reduced to a staminodium. (F) The prohyll develops to a high degree on the lateral and apical portions, enveloping the flower and the glume. (G) Growth of the three stigmas and differentiation of the stamen into filament and anther. (H) Formation of a style over the ovary bearing the three stigmas. Note the staminodium to the left of the ovary. (I) Apical view of a developing flower, showing how the glume is completely covered by the prohyll, which, in turn, envelopes the stamens and stigmas. (J) Front view of the flower at an advanced stage of development, where the stigmatic branches outgrow the two lateral stamens. Abbreviations: a, anther; B, bract; F, flower primordium; f, filament; G, glume; o, ovule; ov, ovary; P, prophyll; s, stamen; sg, stigma; SLP, spikelet primordium; st, style.

In both species, inflorescences are simply spikes of one-flowered spikelets, and the resulting cone resembles a spikelet, hence the use of the term 'pseudo-spikelet' (Haines and Lye, 1983; Goetghebeur and Vorster, 1988). In a majority of Cypereae, spikelets have many flowers, with distichous glumes, and flowers without hypogynous scales (Vrijdaghs, 2006; Muasya et al., 2009b). Cyperoid spikelets are the ultimate branches of the inflorescence, acting both as a morphological and a functional unit (Vrijdaghs et al., 2010). In several Cyperoideae clades, particularly the most derived ones, there is a tendency towards reduction of the spikelets and the inflorescence (Guarise and Vegetti, 2008) and to transfer the spikelet functions to the inflorescence (Vrijdaghs et al., 2010). This happens in the highly derived genera of Cypereae (such as *Ascolepis* and *Lipocharpha*), in which, given the significant reduction of the spikelet, the inflorescence as a whole takes over the spikelet function (=flower function) (Goetghebeur, 1986; Vrijdaghs, 2006; Vrijdaghs et al., 2010).

The floral development in *L. humboldtiana* and *A. brasiliensis* follows the general ontogenetic pattern as it has been observed in all Cyperoideae studied (Vrijdaghs et al., 2004, 2005a,b,c, 2006, 2009, 2010). Primordia of perianth parts are not observed in either species, as is the case with most Cypereae species (Vrijdaghs, 2006), and the abaxial (glume) and the adaxial (prophyll) scales are clearly distinct from a stamen and carpel primordium. The abaxial stamen primordium, which originates with some delay in *L. humboldtiana* and many Cyperoideae, does not appear at all in *A. brasiliensis*, neither does so the second lateral stamen primordium. Such absence

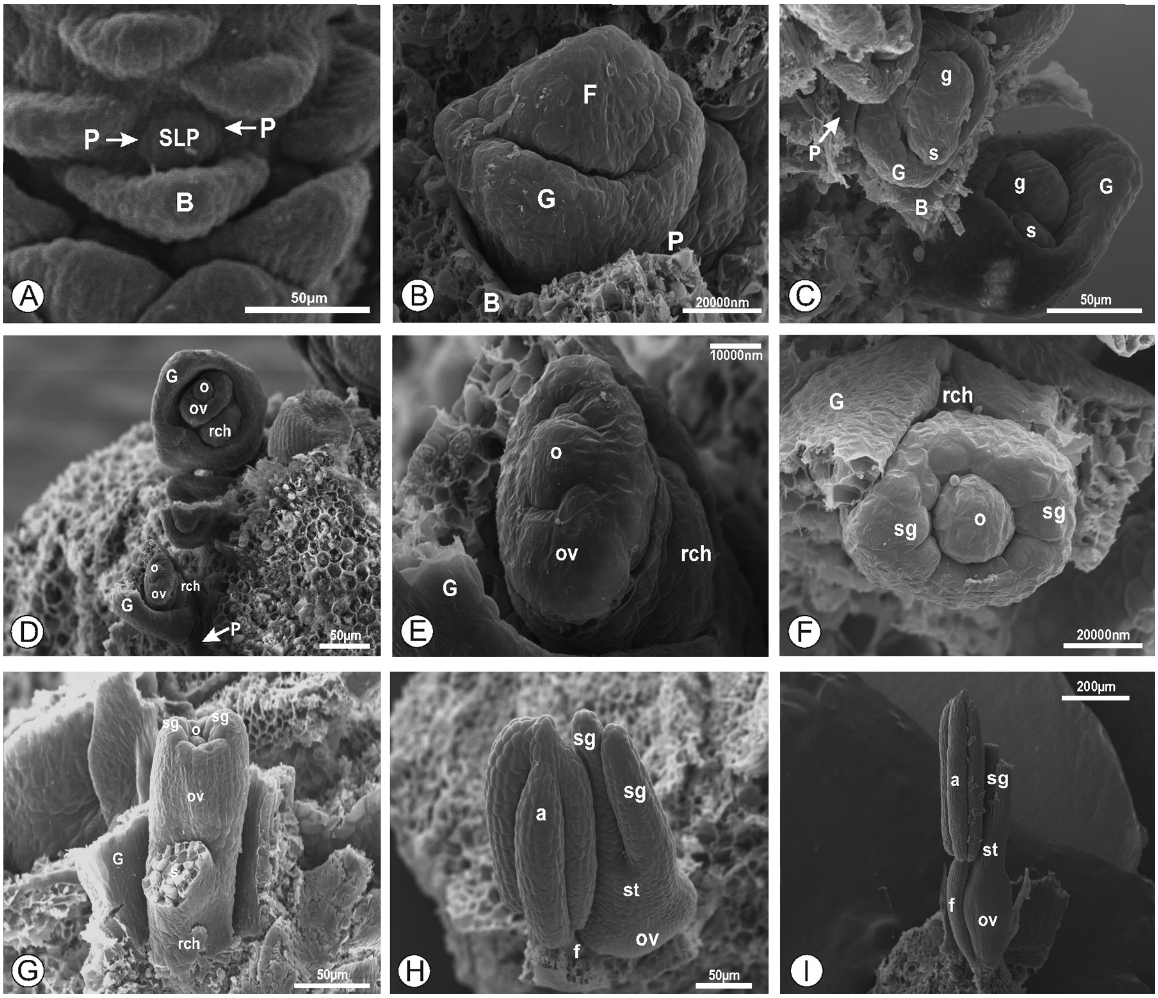

Fig. 4. Spikelet and floral ontogeny in *Ascolepis brasiliensis.* (A) Development of the spikelet primordium and the two lateral bulges of the prophyll in the bract axil. (B) Developing spikelet, where the glume primordium differentiates; growth arrest of the prophyll and adaxial displacement of the apical meristem of the spikelet rachilla. (C) In the floral meristem, the gynoecium primordium and the lateral stamen primordium differentiate, and the glume growth is observed. (D) In the gynoecium, the ovary wall and the only central ovule differentiate. (E) Presence of the rachilla in adaxial position due to the flower displacement. (F) Differentiation of the two stigma primordia on the ovary wall. (G) Growth of the ovary wall and the two stigmas. Presence of a rudimentary rachilla. (H) Lengthening of the two stigmas, which grow as long as the stamen. (I) Front view of the flower at an advanced stage of development. Abbreviations: a, anther; B, bract; F, flower primordium; f, filament; g, gynoecium; G, glume; o, ovule; ov, ovary; P, prophyll; rch, rachilla; s, stamen; sg, stigma; SLP, spikelet primordium; st, style.

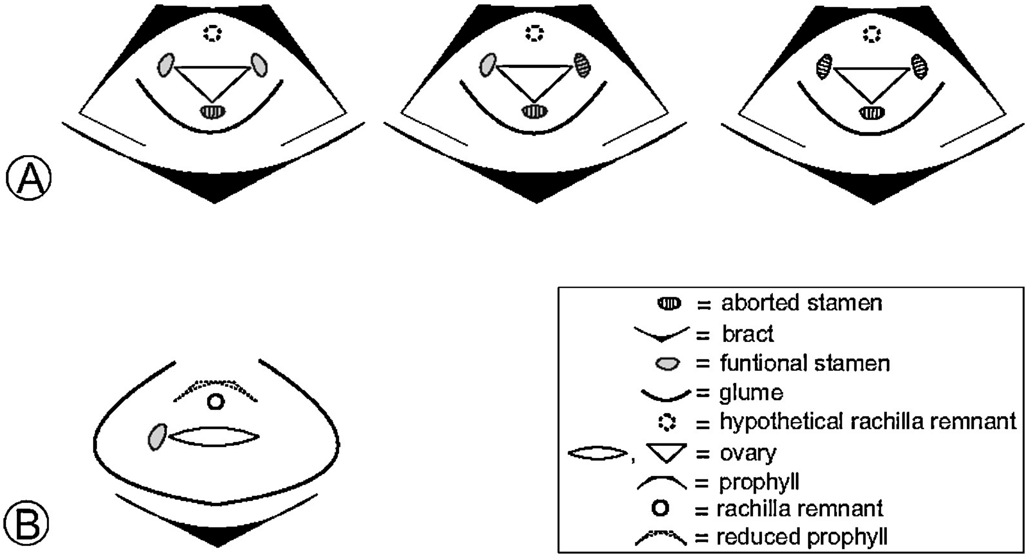

Fig. 5. Spikelet and floral diagram in *Lipocarpha humboldtiana* and *Ascolepis brasiliensis*. (A) L. humboldtiana. (B) *A. brasiliensis*.

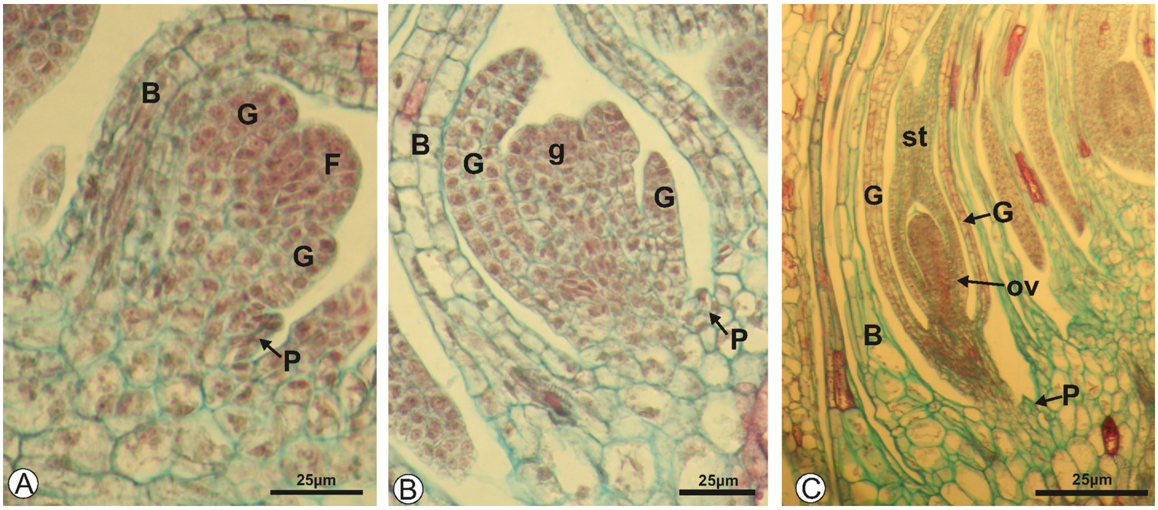

Fig. 6. Single-flowered spikelet in *Ascolepis brasiliensis*. (A–C) Longitudinal view of a single-flowered spikelet, where the prophyll primordium is observed; the prophyll stops growing at an early stage, while the bract, the glume and the flower continue growing. Abbreviations: B, bract; F, flower primordium; G, glume; g, gynoecium; ov, ovary; P, prophyll; st, style.

of development of one or two stamens has been observed also in other Cyperoideae species (Vrijdaghs et al., 2004, 2005a, 2009). These authors have come to the conclusion that the reduction of the abaxial stamen occurred independently in different Cyperoid clades and, in all cases, this tendency can probably be explained by a limited spatial freedom of the stamens to develop. In both studied species, the origin and development of the gynoecium follows the typical pattern of Cyperoid flowers, where, in the earliest developmental stages, the ovary wall originates as a ring primordium surrounding a central ovule primordium, and then, from two (in *A. brasiliensis*) or three (in *L. humboldtiana*) bulges on the top of the rising ovary wall, the stigma branches originate (Vrijdaghs et al., 2009; Reynders et al., 2012).

This work on flower, spikelet and inflorescence development in *L. humboldtiana* and *A. brasiliensis* supports the following hypotheses: (1) hypogyneous scales in developed inflorescences are homologous to the glume and the prophyll; (2) these species present a cyperoid spikelet; (3) the spikelet is certainly monopodial at least in *A. brasiliensis*; (4) the inflorescence is a spike of reduced spikelets; (5) floral ontogeny in *L. humboldtiana* and *A. brasiliensis* follows the general ontogenetic pattern observed in Cyperoideae; (6) the prophyll differentiates in both species, but stops growing at an early stage in *A. brasiliensis*. These characteristics, as evidenced from a development perspective, support the proposed inclusion of both genera with the rest of the Cypereae in molecular phylogenies of the Cyperaceae family (Muasya et al., 1998, 2000, 2009a,b; Simpson et al., 2007).

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