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Ontogeny and structure of the acervulate partial inflorescence in *Hyophorbe lagenicaulis* (Arecaceae; Arecoideae)

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• *Background and Aims* The palm tribe Chamaedoreeae displays flowers arranged in a complex partial inflorescence called an acervulus. This type of partial inflorescence has so far not been reported elsewhere in the largest palm subfamily Arecoideae, which is traditionally characterized by flowers predominantly arranged in triads of one central female and two lateral male flowers. The ontogenetic basis of the acervulus is as yet unknown and its structural diversity throughout the genera of the Chamaedoreeae poorly recorded. This study aims to provide critical information on these aspects.
• *Methods* Developmental series and mature inflorescences were sampled from plants cultivated in international botanical gardens and wild populations. The main techniques employed included scanning electronic microscopy and serial anatomical sectioning of resin-embedded fragments of rachillae.
• *Key Results* Inflorescence ontogeny in *Hyophorbe lagenicaulis* demonstrates that the acervulus and the inflorescence rachilla form a condensed and cymose branching system resembling a coenosome. Syndesmy results from a combined process of rapid development and adnation, without or with reduced axis elongation. Acervulus diversity in the ten taxa of the Chamaedoreeae studied is displayed at the level of their positioning within the inflorescence, their arrangement, the number of floral buds and their sexual expression.
• *Conclusions* The results show that a more general definition of the type of partial inflorescence observed within the large subfamily Arecoideae would correspond to a cyme rather than to a floral triad. In spite of their common cymose architecture, the floral triad and the acervulus present differences with respect to the number and arrangement of floral buds, the superficial pattern of development and sexual expression.

Key words: Arecoideae, Chamaedoreeae, *Hyophorbe lagenicaulis*, acervulus, development, partial inflorescence.

INTRODUCTION

The largest and most diverse palm subfamily, the Arecoideae, has been traditionally characterized by the combination of pinnate leaves and the presence of a particular type of partial inflorescence known as a triad, the latter formed by two staminate flowers flanking one central pistillate flower, or groups reduced from this type of arrangement (Dransfield and Uhl, 1998; Dransfield *et al.*, 2008). However, the presence of the floral triad as an unequivocal synapomorphy for the entire subfamily was questioned after recent palm molecular phylogenies (i.e. Asmussen *et al.*, 2006; Baker *et al.*, 2009) provided solid arguments for placing the tribe Chamaedoreeae in the Arecoideae, the former having been previously included in the subfamily Ceroxyloideae (as Hyophorbeae). The Chamaedoreeae are characterized by a remarkably different type of partial inflorescence known as an acervulus, although solitary flowers or triads have been also reported for the group (Dransfield *et al.*, 2008; Askgaard *et al.*, 2008). Conversely, the tribe Caryoteae was also recently moved to a new subfamily, in this case the Coryphoideae, even though caryotoid palms have also been characterized by the presence of flowers arranged in triads. The present contribution deals with the ontogeny and structural diversity of the acervulus in the tribe Chamaedoreeae.

The latter palm group has raised considerable interest among palm researchers, given its diversity of morphology and sexual expression (it includes both monoecious and dioecious taxa), its unclear phylogenetic position within the Arecoideae, its unresolved intergeneric relationships in spite of repeated molecular phylogenetic efforts and its enigmatic phytogeographical pattern, displaying one of the most extraordinary cases of disjunction in the palm family. Some of the diagnostic characters assigned to the group include the presence of an acervulus or derivatives of this type of partial inflorescence, lack of bracts and bracteoles in the inflorescence at maturity, small, polysymmetric flowers and a trilocular, triovulate gynoecium with ovules laterally attached (Uhl and Moore, 1978; Dransfield and Uhl, 1998; Dransfield *et al.*, 2008). The Chamaedoreeae include the genera *Hyophorbe* (five species), *Gaussia* (five species), *Synechanthus* (two species), *Chamaedorea* (110 species) and *Wendlandiella* (one species); the latter four genera are distributed from southern Mexico to the northern part of South America and the Caribbean (Hodel, 1992; Henderson *et al.*, 1995; Dransfield and Uhl, 1998). Only one genus (*Hyophorbe*) is from the Old World, endemic to the Mascarene Islands in the Indian Ocean (Dransfield *et al.*, 2008). A relatively basal position for Chamaedoreeae has been proposed in at least

two molecular phylogenies (Hahn, 2002*a*; Baker *et al.*, 2009), which resolved with moderate support a position for the tribe Chamaedoreeae as sister to all Arecoideae except the Iriarteeae. The monophyly of the Chamaedoreeae has been supported by several studies (i.e. Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen and Chase, 2001; Hahn, 2002*a*, *b*; Lewis and Doyle, 2001, 2002; Asmussen *et al.*, 2006; Thomas *et al.*, 2006; Cuenca and Asmussen-Lange, 2007; Cuenca *et al.*, 2008; Baker *et al.*, 2009). The study of Cuenca *et al.* (2009) additionally proposed monophyly for individual genera, but relationships among them were resolved with only low to moderate support.

The Latin term 'acervulus' means 'heap of things' and was never employed in classical treatments of inflorescence classification such as Troll (1964, 1969) or Weberling *et al.* (1993). In fact, it has been rather employed in mycology to define a cluster of cells bearing spores of non-Hymenomycetes fungi. A rough description of this type of partial inflorescence in palms was provided by Corner (1966) who mentioned that genera such as *Hyophorbe* and *Synechanthus* produced four or five flowers in the axil of every bract of the rachilla, and these opened in basipetal succession. The term acervulus was first explicitly used in the palm family by Moore (1971)

in his study of the genus *Synechanthus*. Moore described the acervulus as an unusual partial inflorescence in which the basal-most flower was usually female, and two to several male flowers were borne above it in a line, clearly making reference to its heap-like construction. Uhl and Moore (1978) further interpreted the acervulus as a form of cincinnus in which the flowers were arranged in a double row of two to ten or more, closely appressed, sessile flowers. The acervulate partial inflorescence of the Chamaedoreeae has been identified so far in all the monoecious genera (*Gaussia*, *Hyophorbe*, *Synechanthus*), but is restricted to the staminate inflorescences in the dioecious genera *Wendlandiella* and *Chamaedorea* (Uhl and Moore, 1978; Dransfield and Uhl, 1998; Dransfield *et al.*, 2008), in the latter only reported in three of the 110 species that compose the genus (Thomas *et al.*, 2006). The most recent taxonomic account of the palm family (Dransfield *et al.*, 2008) has defined the acervulus as an inverted type of cincinnus.

Developmental data on the arecoid floral triad have been recently published for commercially important species such as *Cocos* (Perera *et al.*, 2010) and *Elaeis* (Adam *et al.*, 2005), but almost nothing is known about inflorescence development in other arecoid palms. Moreover, apart from the study
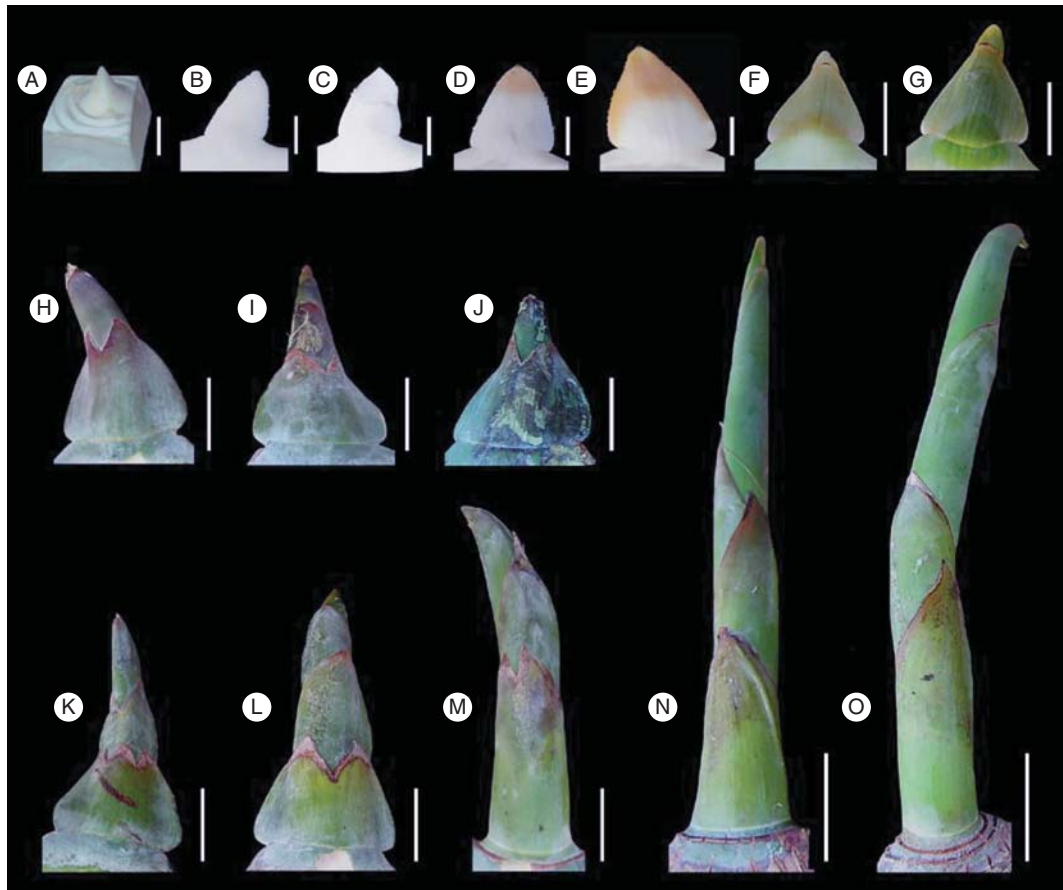

FIG. 1. Early inflorescence development in *Hyophorbe lagenicaulis*. Eight informative stages were retained for the study (H−O) from a total of 15 sampled. (A) Inflorescence primordium attached close to the palm vegetative apex. (B−E) Immature axillary buds showing early prophyll initiation. (F, G) Inflorescence bud shortly after prophyll and first peduncular bract initiation. (H−L) Inflorescence buds showing prophyll and peduncular bract initiation. (M−O) Late inflorescence buds showing elongation of prophyll and peduncular bracts. Scale bars: (A−E) = 0·5 cm; (F−J) = 2 cm; (K−M) = 3 cm; (N−O) = 4 cm.

describing selected developmental stages of acervuli in *Hyophorbe indica* (Uhl and Moore, 1978), relatively few data have been obtained on the ontogeny of this type of partial inflorescence. Two major elements have traditionally made the acervulus a difficult subject to study: (1) the lack of obvious pherophylls (subtending bracts) for individual flowers, as already reported in plant families such as the Brassicaceae (Hagemann, 1963), Papilionoideae (Prenner, 2004), Poaceae (Vegetti and Weberling, 1996), Araceae (Buzgo, 2001), Hydatellaceae (Rudall *et al.*, 2007) and Nympheaceae (Endress and Doyle, 2009), has strongly hindered the interpretation of the general architecture of the acervulus; (2) the basipetal direction of development displayed by the acervulus differs from the acropetal ontogenetic progression seen in its architecture, leading to equivocal interpretations with respect to its origin and, hence, to its type of branching system.

The apparent structural contradiction between the two types of partial inflorescences occurring in the Arecoideae (floral triad vs. acervulus) has prompted us to undertake the first complete ontogenetic study of the acervulus in a member of the tribe Chamaedoreeae (*Hyophorbe lagenicaulis*), in order to better understand its specific developmental pattern. Moreover, the structure of the acervulus is interpreted in the context of modern literature on inflorescence architecture and the diversity observed in members of all genera of the tribe is discussed with the aim of exploring its value with respect to intergeneric

relationships within the Chamaedoreeae. Details on the floral structure of all species studied are not provided here since they will be presented in a separate paper dealing with floral structure and systematics in the tribe Chamaedoreeae (N. Ortega-Chávez and F. W. Stauffer, unpub. res.).

MATERIALS AND METHODS

Plant material

For the ontogenetic study of *Hyophorbe lagenicaulis* (L.H. Bailey) H.E.Moore, 15 inflorescences at different stages of development were sampled from a single individual cultivated in the Conservatory and Botanical Garden of Geneva (Fig. 1). Only the last eight stages from this complete developmental series proved to be informative for the study (Fig. 1H–O). Pre-anthetic and anthetic stages were obtained from an individual of the Royal Botanic Gardens, Kew. For the comparative study of mature acervuli in members of the Chamaedoreeae, entire rachillae or fragments thereof were studied in ten taxa, representing all genera of the tribe (Table 1). The *Chamaedorea* species selected were those described by Thomas *et al.* (2006) as bearing acervuli; however, non-acervulate species in the genus were also preliminarily studied. Fresh, liquid-fixed and dried material of the five genera of Chamaedoreeae were obtained from various herbaria (AAU, BH, C, F, G, K, LPB, MO, NY, US, USM and

TABLE 1. *Plant material studied*

Species	Origin	Collection data	Material
Hyophorbe lagenicaulis (L.H. Bailey) H.E. Moore	Conservatory and Botanical Garden of Geneva, Switzerland	Stauffer (06/2008)	Fresh
	Royal Botanic Gardens, Kew, UK	No. 087−83·00674	Fresh
		No. 2000−4396	Fresh
	University of Copenhagen, Denmark	s.d. (12/07/2004)	Liquid-fixed
	Montgomery Botanical Center, USA	91110*U	Fresh
Hyophorbe verschaffeltii H. Wendl.	Montgomery Botanical Center, USA	931087*C	Fresh
	Royal Botanic Gardens, Kew, UK	No. 45949	Liquid-fixed
Gaussia maya (Cook) H.J. Quero & Read	Royal Botanic Gardens, Kew, UK	No. 45951	Liquid-fixed
		No. 801−58·80101	Fresh
	University of Copenhagen, Denmark	s.d. (08/07/2004)	Liquid-fixed
		s.d. (12/07/2004)	
		s.d. (15/07/2004)	
		s.d. (19/07/2004)	
Gaussia princeps H. Wendl.	University of Copenhagen, Denmark	s.d. (08/07/2004)	Liquid-fixed
Synechanthus warscewiczianus H. Wendl.	University of Copenhagen, Denmark	s.d. (20/07/2004)	Liquid-fixed
	University of Aarhus, Denmark	No. 62015, No. 62021, No. 62193	Liquid-fixed
Synechanthus fibrosus H. Wendl.	Fairchild Tropical Garden, USA	2001 0842*E	Fresh
Chamaedorea microspadix Burret	Conservatory and Botanical Garden of Geneva, Switzerland	Ortega & Stauffer (02−04/2010)	Fresh
	University of Aarhus, Denmark	Hodel No. 945	Liquid-fixed
		Hodel No. 759	Liquid-fixed
Chamaedorea linearis Mart.	University of Aarhus, Denmark	No. 39, No. 97875, No. 62008, No. 62092	Liquid-fixed
	Royal Botanic Gardens, Kew, UK	No. 44428·00	Liquid-fixed
Chamaedorea radicalis Mart.	University of Aarhus, Denmark	Hodel No. 793	Liquid-fixed
		Hodel No. 809	Liquid-fixed
Wendlandiella gracilis var. *gracilis* Dammer	University of Halle−Wittemberg, Germany	Ktach & Röser (02/2010)	Fresh
Wendlandiella gracilis var. *polyclada* (Burret) A. Hend.	Iquitos−Peru	Vargas (02/2010)	Fresh

WU) as well as living botanical garden collections from the Conservatory and Botanical Garden of Geneva (CJB), Royal Botanic Gardens, Kew (K), Fairchild Tropical Botanic Garden (FTG), Montgomery Botanical Center (MBC) and the University of Halle-Wittenberg. A field trip to Peru was carried out in October 2009 with the aim of collecting inflorescences in species of *Wendlandiella* Dammer.

Macro-morphology and scanning electron microscopy (SEM)

Inflorescences at different stages of development from *Hyophorbe lagenicaulis* and fragments of inflorescences from other members of the Chamaedoreeae were collected and fixed in FAA for the ontogenetic and comparative studies of the acervulus, respectively. Rachillae were dissected under a stereomicroscope (Kombistereo, Wild
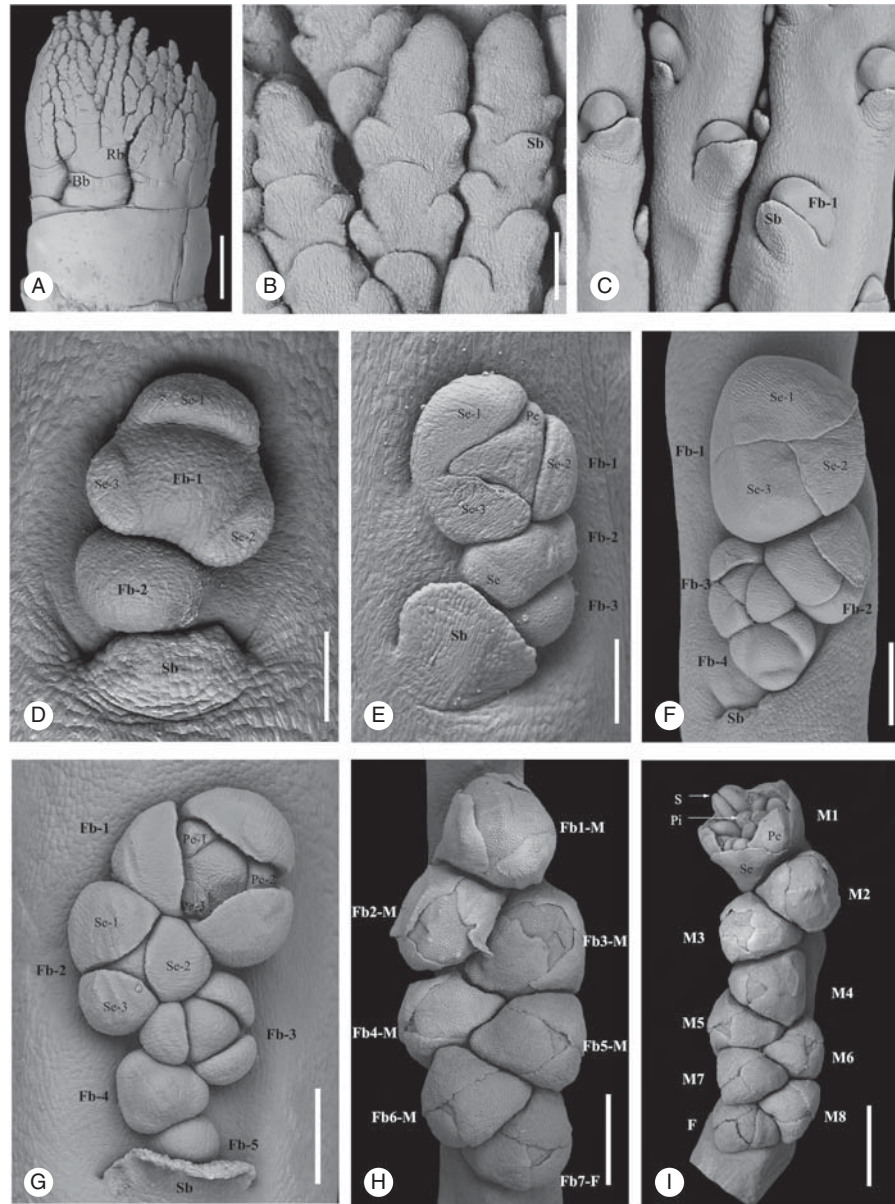

FIG. 2. SEM developmental study of the acervulus in *Hyophorbe lagenicaulis*. (A) Complete inflorescence at stage I (corresponding to H in Fig. 1) showing the already differentiated rachis and rachillae. (B) Detail of rachillae at stage I showing spirally arranged subtending bracts. (C) Portion of rachilla at stage II showing the subtending bract and the first developing floral bud of the acervulus. (D) Portion of rachilla at stage III showing the subtending bract and two developing floral buds; the first male bud is starting sepal differentiation. (E) Portion of rachilla at stage IV showing the subtending bract and three male floral buds in sequential development; the first male bud is starting petal differentiation, whereas the second male bud starts sepal differentiation. (F) Portion of rachilla at stage V showing a reduced subtending bract and four floral buds in sequential development. (G) Portion of rachilla at stage VI showing the subtending bract and five floral buds in sequential development; sepals and petals are completely differentiated in Fb-1. (H) Portion of rachilla at stage VIII showing an acervulus with seven floral buds in sequential development; perianth completely developed in Fb-1. (I) Portion of rachilla at stage X showing a mature acervulus; the uppermost male flower has reached the point of anthesis. Scale bars: (A, I) = 1 mm; (B–G) = 100 μm; (F) = 200 μm; (H) = 800 μm. Abbreviations: An, anther; Bb, branch bract; Br, rachillae bract; F, female flower; Fb-1, first floral bud; Fb-2, second floral bud; Fb-3, third floral bud; Fb-4, fourth floral bud; Fb-5, fifth floral bud; Fb1-M–Fb6-M, male floral buds; Fb7-F, female floral bud; M1–M8, male flowers; Pe, petal; Pe-1, first petal; Pe-2, second petal; Pe-3, third petal; Pi, pistillode; Sb, flower subtending bract; Se, sepal; Se-1, first sepal; Se-2, second sepal; Se-3, third sepal.

HEERBRUGG/ M3Z – Switzerland) and samples for SEM were dehydrated, critical-point dried and sputter-coated with gold for observations using a Zeiss DSM 940A – Orion 6·60 Imaging System at the Natural History Museum of Geneva.

Histological and anatomical analyses

A complete series of different developmental stages were selected for *Hyophorbe lagenicaulis* and mature acervuli containing flowers in late bud or anthesis were chosen for the comparative study in other members of the tribe. In all cases
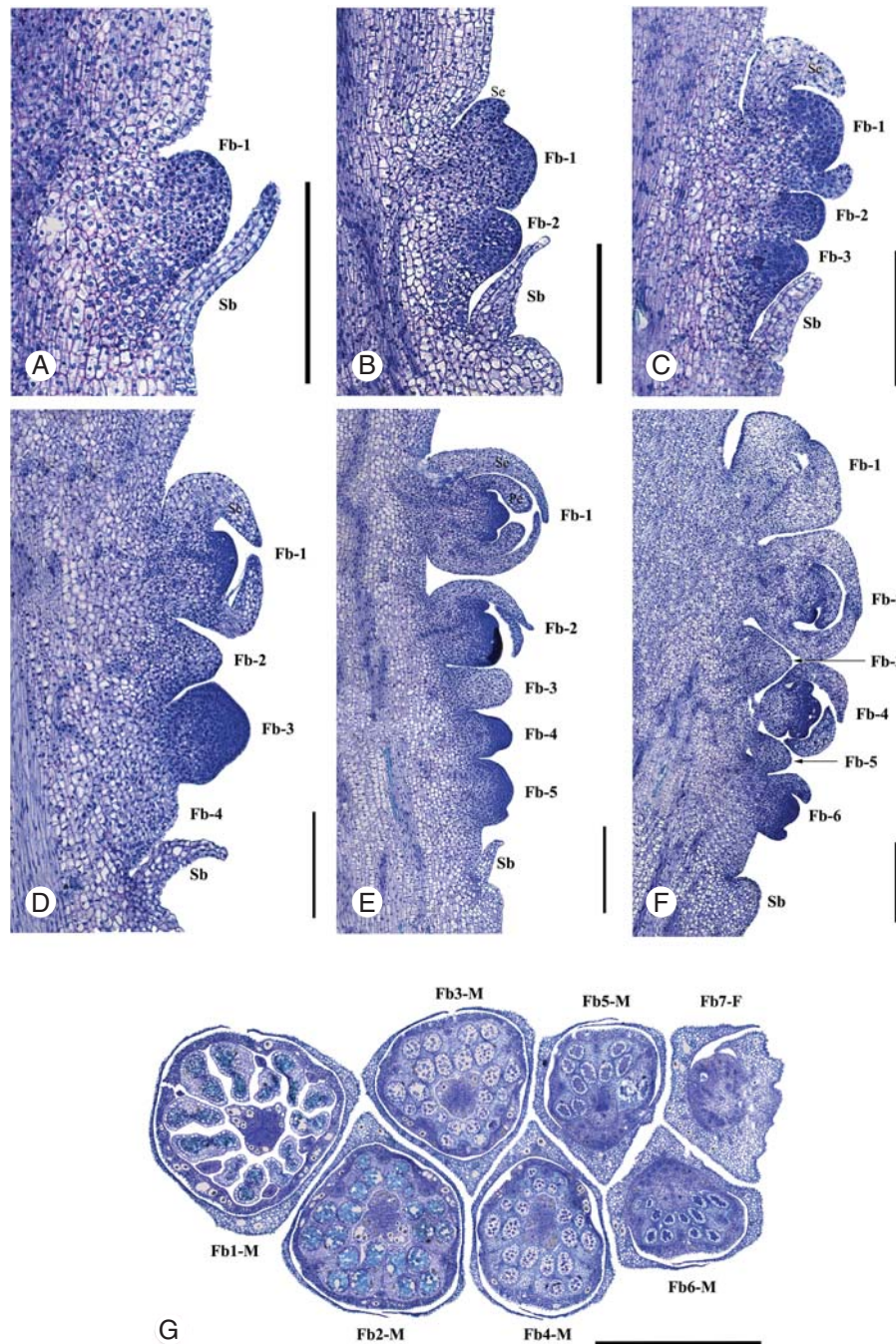

FIG. 3. Histological study of acervulus development in *Hyophorbe lagenicaulis* (A–F, longitudinal sections; G, cross-section). (A) Section of rachilla at stage II showing the acervulus subtending bract and the first developing male floral bud. (B) Section of rachilla at stage III showing the acervulus subtending bract and two developing floral buds. (C) Section of rachilla at stage IV showing the subtending bract and three floral buds; sepals are clearly differentiated in Fb-1. (D) Section of rachilla at stage V showing a reduced subtending bract and four floral buds. (E) Section of rachilla at stage VI showing a strongly reduced subtending bract and five floral buds; Fb-1 starts androecium differentiation. (F) Section of rachilla at stage VII showing six floral buds. (G) Cross-section of acervulus at stage VIII showing seven floral buds in sequential development. Scale bars: (A–F) = 100 μm; (G) = 500 μm. Abbreviations: Fb-1, first floral bud; Fb-2, second floral bud; Fb-3, third floral bud; Fb-4, fourth floral bud; Fb-5, fifth floral bud; Fb-6, sixth floral bud; Fb1-M–Fb6-M, male floral buds; Fb7-F, female floral bud; Pe, petal; Sb, subtending bract of the acervulus; Se, sepal.

samples were evacuated and then dehydrated and embedded in Kulzer's Technovit 7100 [2-hydroxyethyl metacrylate (HEMA)] (Igersheim and Cichocki, 1996). The material was serially cross and longitudinally sectioned at 6–8 μm using a rotary microtome (Leitz 1512), stained with ruthenium red and toluidine blue, and enclosed in Histomount. Observations and photographs were carried out with an electronic microscope (NIKON Eclipse 80i) at the Laboratory of Micro-Morphology (CJB) and the Laboratory of Cytology and Vegetal Histology (University of Geneva); the permanent slides were deposited at the Laboratory of Micro-Morphology of the Conservatory and Botanical Garden of Geneva.

RESULTS

Ontogenetic study of the acervulus in Hyophorbe lagenicaulis

Stage I. The entire inflorescence with first- and second-order branches is already well differentiated; each branch and some rachillae show basal bracts (Fig. 2A). On each rachilla there are several well-defined and spirally arranged bracts. The bract subtends the acervulus and offers protection to the meristematic zone from which flowers will differentiate. These bracts are not present towards the apex of the rachilla, which might be linked to the lack of future acervuli in this zone (Fig. 2B).

Stages II–III. At stages II and III a first floral bud emerges from the subtending bract (Fig. 2C). The rachilla is seen to have undergone at least two different modifications; the youngest flower has emerged from the axil of the subtending bract whereas the distal-most region of the acervulus appears somewhat sunken (Fig. 3A). As mentioned for stage 1, the subtending bract continues to protect the acervulus' proximal end. At stage II the first flower further develops and the differentiation of floral organs has started, as witnessed by the presence of three sepals, which appear sequentially (Fig. 2D). Also at this stage the second flower develops, always emerging from the meristematic zone between the subtending bract and the adjacent flower (Fig. 3B). The subtending bract is well developed or in some cases appears reduced in size (Fig. 3E). At this early stage anatomical evidence confirms the total absence of floral bracts for individual flowers (Fig. 3B–F).

Stages IV–V. At stage IV the first developed flower starts to display petal differentiation, whereas the second flower has initiated sepal differentiation. The third floral bud emerges from the acervulus proximal end. The acervulus starts to clearly display a zigzag developmental pattern, enabling additional space for each subsequent floral primordium (Figs 2E and 3C). At stage V the acervulus consists of four floral buds; the upper one is clearly more developed than the lower ones. The first and second floral buds in development

TABLE 2. *Summary of diagnostic characters to differentiate the acervuli in taxa of Chamaedoreeae*

| Species | General disposition of acervuli in the inflorescence | | Arrangement of the flowers within the acervulus | | | | | Sexuality and number of flowers in the acervulus | | |
	Distribution	Type of insertion	Linear	Double row	Triangle	Short spiral	Unordered pattern	Base of rachilla	Apex of rachilla	Figures
Hyophorbe lagenicaulis	1st order branches	Partially sunken	.	x	.	.	.	Bisexual (6–9)	Male (2–3), not all fully developed	2A–I, 3A–G, 6
H. veschaffeltii	1st order branches	Superficial	x	.	.	.	.	Bisexual (5–6)	Male (4)	4A, 6
Gaussia maya	1st order branches	Superficial	x	.	x	.	.	Bisexual (2–3)	Male (2–3), not all fully developed	4B, C, 6
G. princeps	1st order branches	Superficial	x	.	.	.	.	Bisexual (5)	Bisexual or male (3–4)	4D, 6
Synechanthus fibrosus	1st and 2nd order branches	Superficial	x	.	.	.	.	Bisexual (7–8)	Male (5–6), not all fully developed	4E, 6
S. warscewiczianus	1st order branches	Partially sunken	x	.	.	.	.	Bisexual (9–11)	Male (4–6), not all fully developed	6
C. microspadix (♂)	1st order branches	Superficial	.	.	.	x	x	Male (13)	Male (5–6)	6
C. microspadix (♀)	1st and 2nd order branches	Partially sunken	x	.	.	.	.	Female (1–2)	Male (1)	4F, 6
C. radicalis (♂)	1st order branches	Superficial	.	.	.	x	.	Male (2–3)	Male (2–3)	5A, 6
Chamaedorea linearis (♂)	1st order branches	Superficial	x	.	.	.	.	Male (2–3)	Male (2–3)	5B, 6
Wendlandiella gracilis (♂)	1st order branches	Superficial	.	x	.	.	x (rarely)	Male (7–8)	Male (3)	5C, D, 6
W. polyclada (♂)	1st order branches	Superficial	.	x	.	.	.	Male (5–7)	Male (3)	6
W. polyclada (♀)	1st order branches	Partially sunken	x	.	.	.	.	Female (1–2)	Female (1)	6

are completely enveloped by the sepals and the youngest bud is starting to differentiate. The acervulus almost attains the width of the rachilla and the buds display a well-defined zigzag arrangement in which the younger flowers appear to push the earlier formed ones in an acropetal pattern with respect to the rachillae. As a consequence, the more-developed flowers are no longer sunken, whereas the younger flowers remain slightly sunken (Figs 2F and 3D).

Stages VI and VII. At these stages the acervuli consist of five or six flowers and have almost completed their development. The older buds show completely differentiated sepals and petals (Fig. 2G). The uppermost buds start to display differentiation of the androecium (Fig. 3E). The subtending bract of the acervulus now appears reduced in size but small vascular traces show that it is still present (Fig. 3E, F).

Stage VIII. The acervuli consist of seven floral buds. The acervuli in this species are bisexual (with several male flowers and one female flower), but unisexual acervuli (containing only male flowers) also occur, mainly towards the apical zone of the rachillae. The upper flowers are male and the lowest flower (next to the subtending bract) is the only female one (Fig. 2H). Protandry is observed in the acervulus; the anthesis of male flowers clearly precedes the maturity of the female flower; the oldest male bud is the first to reach anthesis and the next bud will start opening when the previous one is completely open (Fig. 3G).

Stages IX–X. By this point the acervuli have completely developed. Eight or nine flowers are the highest number identified in the samples studied; the uppermost flower is seen to have started anthesis, whereas the remaining ones at the base and in the middle region continue their development (Fig. 2I). The female flower will reach maturity after all the male flowers have been shed. The acervulus has by now reached its maximal length; the subtending bract is completely reduced and in some cases it can be entirely hidden by the last bud to develop.

Comparative structure of the acervulus in other members of the Chamaedoreeae

To provide a comparative morphological and anatomical framework for the acervulus structure described in *Hyophorbe lagenicaulis* additional data are presented on the acervuli of other taxa of the Chamaedoreeae studied. The
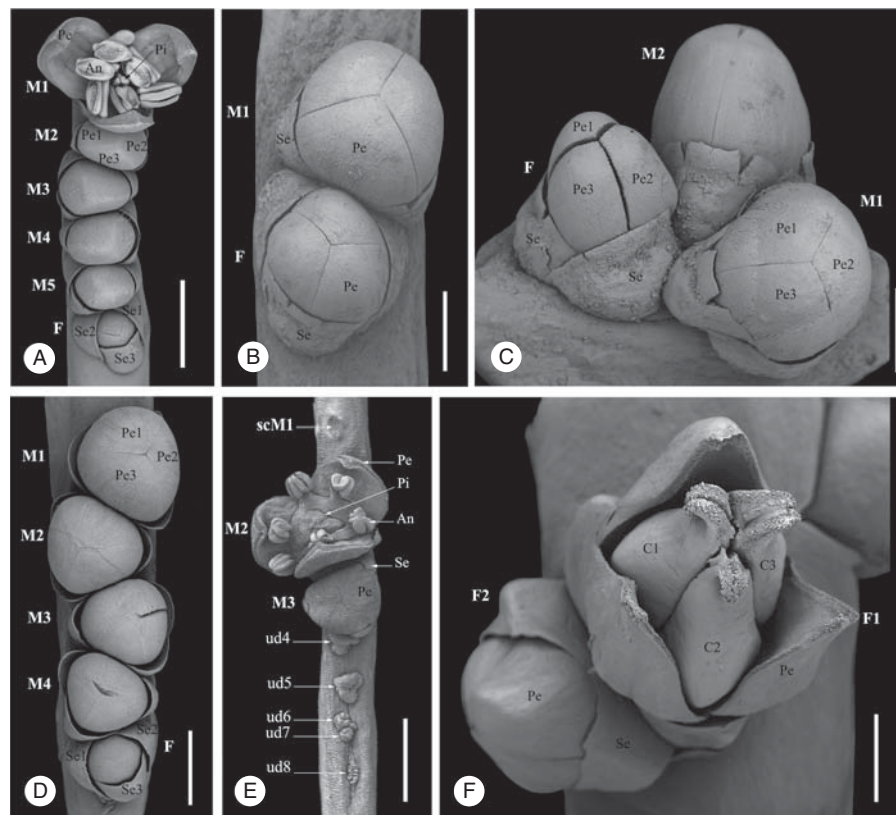

F<small>IG</small>. 4. Structural diversity of acervuli in the tribe Chamaedoreeae. (A) Upper view of a six-flowered acervulus in *Hyophorbe verschaffeltii*; the uppermost male flower (M1) has reached the point of anthesis. (B) Upper view of a two-flowered acervulus in *Gaussia maya* showing a lower female flower and an upper male flower. (C) Lateral view of a three-flowered acervulus in *Gaussia maya* showing a lower female flower and two upper male flowers. (D) Upper view of a five-flowered acervulus in *Gaussia princeps* showing a zigzag arrangement. (E) Upper view of a partially developed acervulus in *Synechanthus fibrosus*. (F) Portion of a female rachilla in *Chamaedorea microspadix* with a two-flowered female acervulus; the upper flowers at full anthesis. Scale bars: (A) = 1·5 mm; (B, D) = 1 mm; (C) = 700 μm; (E) = 900 μm; (F) = 800 μm. Abbreviations: An, anther; Ca1–Ca3, carpels; F, female flower; F1 and F2, female flowers; M1–M5, male flowers; M2, second male flower; M3, third male flower; Pe, petal; Pe1–Pe3, differentiated petals; Pi, pistillode; scM1, scar left by male flower; Se, sepal; Se1–Se3, differentiated sepals; ud4–ud8, undeveloped buds.
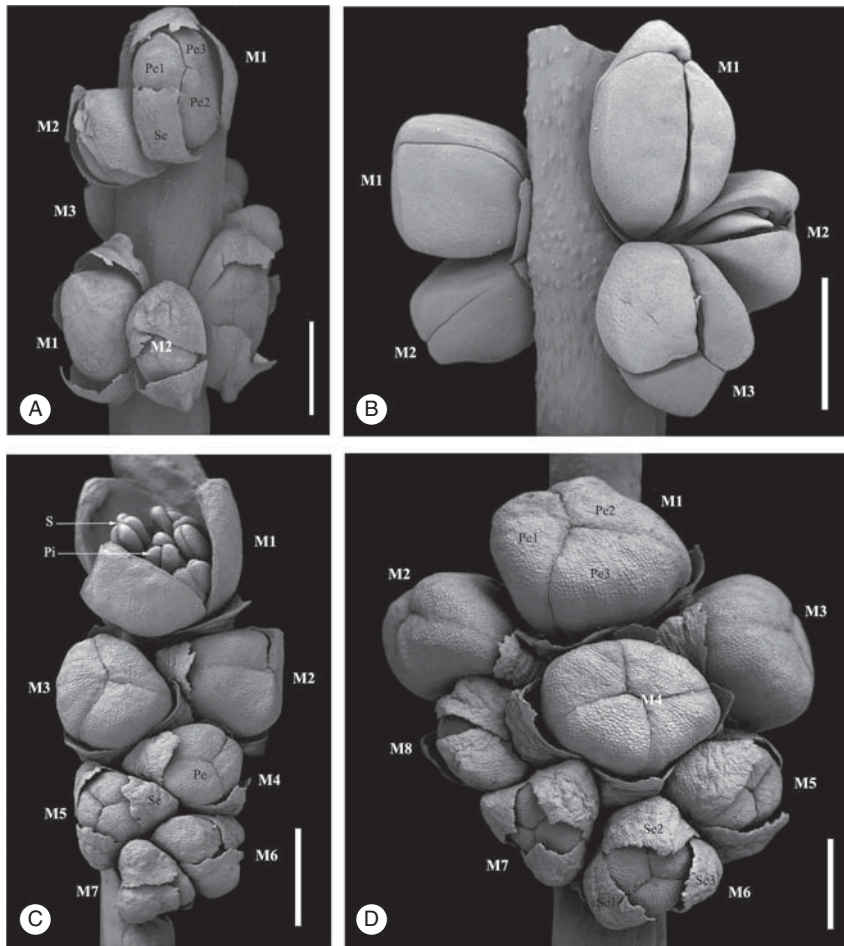
FIG. 5. Structural diversity of acervuli in the tribe Chamaedoreeae. (A) Upper view of a two-flowered (top) and a tree-flowered (bottom) acervulus in *Chamaedorea radicalis*. (B) Upper view of a two-flowered (left) and a three-flowered acervulus (right) in *Chamaedorea linearis*. (C, D) Upper view of acervuli in *Wendlandiella gracilis* var. *gracilis*. (C) Seven-flowered acervulus showing buds arranged in zigzag. (D) Eight-flowered acervulus showing unordered arrangement of the buds. Scale bars: (A) = 1·3 mm; (B) = 1·4 mm; (C) = 800 μm; (D) = 500 μm. Abbreviations: M1–M8, male flowers; Pe1–Pe3, petals differentiated; Pe, petal; Pi, pistillode; S, stamen; Se, sepal; Se1–Se3, sepals differentiated.

main diagnostic characters that can be used to differentiate the acervuli in the taxa investigated are summarized in Table 2 and illustrated in Figs 4 and 5.

DISCUSSION

The acervulus and the floral triad

The acervulus of the Chamaedoreeae is a type of partial inflorescence that in more general terms should be regarded as a monochasial cyme. The acervulus and the rachilla form a coenosome (as discussed by Endress, 2010), which represents a condensed branching system resembling a solid body, a syndesmic process that has been described for the compact inflorescences of *Cordia* (Hagemann, 1975) or *Ficus* (Bernbeck, 1932). The present ontogenetic study of the acervulus in *Hyophorbe lagenicaulis* demonstrates that syndesmy of the acervulus is characterized by a rapid process of development and adnation, without or with reduced axis elongation. It is now clear that the acervulus cannot be considered as a raceme or spike, as suggested by Corner (1966), due to its

basipetal pattern of development, characteristic of the sympodial systems. A more general definition of the floral triad characterizing most arecoid tribes corresponds to that of a cyme (as defined by Troll, 1964, 1969; Müller-Doblies and Müller-Doblies, 1987; Endress 2010), which also reflects the structure and ontogenesis observed in the acervulus. Hence, the presence of a partial cymose inflorescence, rather than that of floral triads, would better explain the dominant inflorescence type within the Arecoideae. In spite of their common cymose architecture, the two types of partial inflorescence observed in the Arecoideae display important differences, particularly with respect to their sexual expression, floral maturation sequence, number and arrangement of floral buds, and superficial pattern of development (Table 3).

The present phylogenetic framework for the palm family has largely surpassed our knowledge of the ontogeny and structure of the main types of partial inflorescences characterizing the arecoid tribes, making it difficult to address the question of evolutionary directions. How the syndesmic acervuli and the triads could be derived from a common ancestor and

TABLE 3. *Main differences between the two dominant types of partial inflorescences in the palm subfamily Arecoideae*

|	Triad	Acervulus
Taxonomical distribution	13 tribes and 102 genera	One tribe and five genera
Generic sexual expression	Restricted to monoecious genera	Dominant in monoecious genera and in dioecious genera almost restricted to male inflorescences
Sexual expression	Bisexual	Bisexual or unisexual (mostly male flowers)
Reported sequence of floral anthesis	Protandry or protogyny	Protandry (in monoecious genera). Simultaneous anthesis of male and female flowers only rarely observed
Number of floral buds concerned	Three floral buds or derivate groups of dyads or solitary flowers. Reduction in number towards the apex of the rachilla	Between two and 13 floral buds. Reduction in number towards the apex of the rachilla
Dominant arrangement of the flowers	One central female flower flanked by two lateral male flowers	One or two female flowers next to the subtending bract of the acervulus and one to 12 male flowers in distal position
Superficial pattern of development observed	Acropetal	Basipetal
Subtending bracts of individual floral buds	Always present	Not differentiated or inconspicuous
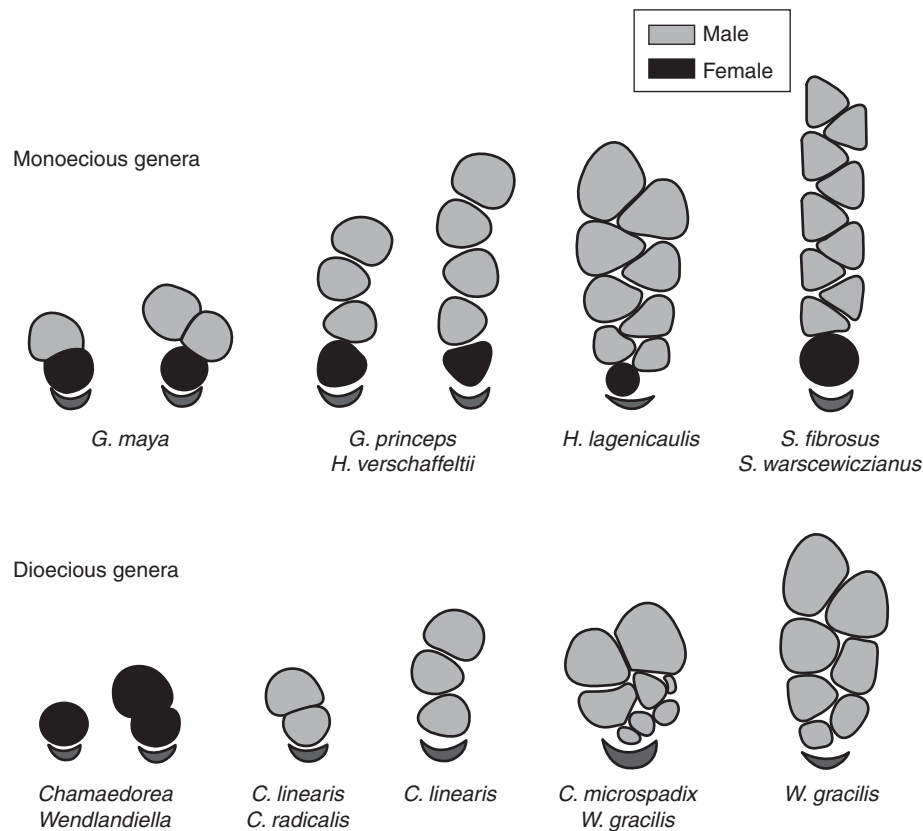
FIG. 6. Acervulus diversity in monoecious and dioecious genera of Chamaedoreeae. Arrangement proposed according to the number of floral buds present in the acervulus. Male floral buds are shaded grey, female are black.

whether the acervulus could be regarded as the plesiomorphic condition for the partial inflorescences seen in the Arecoideae are questions that will require more and wider structural and ontogenetic studies.

Structural diversity of the acervulus

A considerable range of acervulus diversity, especially with respect to the number and arrangement of the floral buds, was observed in the ten taxa of Chamaedoreeae studied here (Table 2, Figs 4 and 5), making it relatively difficult to infer any relationships within the tribe. In the monoecious genera, the acervuli show a regular arrangement of floral buds (linear, zigzag in double row, or triangle-shaped), whereas in the dioecious genera, the floral buds in the acervuli display a large diversity of arrangements, ranging from linear, zigzag in double row or spirals to more complicated arrangements with no obvious recognizable pattern (Fig. 6). In *Hyophorbe*

the floral buds of the acervuli can display either a linear or a clearly double row arrangement. Most *Gaussia* species show a linear acervulus, but in some acervuli of *G. maya* the floral buds contain three flowers (one female and two male), which suggests some superficial resemblance with the classical arecoid floral triad; however, Uhl and Moore (1978) found anatomical evidence supporting its acervulate origin. Low morphological diversity was identified in the acervuli of the genus *Synechanthus*, which could be distinguished from the rest of the genera by the presence of floral buds arranged in a zigzag pattern and the triangular shape of the male flowers.

The arrangement of the flowers observed in male inflorescences of *Chamaedorea*, in many cases characterized by densely packed floral clusters, does not allow the recognition of any obvious pattern and its interpretation remains difficult. For the acervulate taxa of *Chamaedorea* studied, it was observed that *C. linearis* displayed linear acervuli composed of two or three floral buds (sometimes similar to those observed in *G. maya*), whereas in *C. radicalis* it is difficult to define the predominant type of partial inflorescence because the floral buds develop almost in a tight spiral; *C. microspadix* displays few clearly defined acervuli at the base of the rachillae and towards the apex the acervuli are replaced by floral clusters without a recognizable type of arrangement. *Wendlandiella* displays acervuli with floral buds arranged in a double row (similar to the type observed in *Hyophorbe*); however, in a few cases the same unordered type of floral clusters, as observed in *Chamaedorea*, could be identified.

Some genera of the Attaleinae (i.e. *Cocos, Syagrus*) and Bactridinae (i.e. *Acrocomia*) are characterized by inflorescences with floral triads in the lower half of the rachillae, whereas male dyads or solitary male flowers occupy the upper half. This male tendency towards the apical region of the rachilla was also observed in monoecious genera of the Chamaedoreeae, but expressed at the acervulus level. Unisexuality is displayed in two different ways: (1) the acervuli were formed by apparently viable and exclusively well-developed male flowers; and (2) the one to four upper male flowers of the acervulus are normal and develop fully, whereas the lower ones remain vestigial. The protandrous pattern of the acervuli is dominant in the tribe Chamaedoreeae, but in inflorescences of *G. maya* several acervuli displayed female and male flowers at synchronous maturity, or even female maturity clearly preceding that of the male flower. The apparent transition from bisexual to unisexual acervuli may underlie the origin of the dioecious condition observed in *Chamaedorea* and *Wendlandiella*, but further studies are required to confirm this hypothesis. Developmental genetic studies of this transition would complement current efforts dealing with the study of sex determination in angiosperms and the evolution of dioecy in the palm family.

ACKNOWLEDGEMENTS

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