Original article

Different ontogenetic processes promote dicliny in *Ficus* L. (Moraceae)

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ABSTRACT

The absence of reproductive organs in flowers may ontogenetically arise from inception or by abortion during development. *Ficus* L., a species-rich genus of angiosperms, is an interesting model for floral developmental studies because of the diversity of sexual systems it contains. This study compares the floral morphology of *Ficus citrifolia* (monoecious), *Ficus religiosa* (monoecious), *Ficus racemosa* (secondarily monoecious), and *Ficus hispida* (gynodioecious) across development to establish the ontogenetic pathways that result in diclinous flowers. Figs were collected at various developmental stages and were prepared for surface (scanning electron microscopy) and histological (light microscopy) analyses. Dicliny in *Ficus* is defined by stamen absence from inception in pistillate flowers and either pistil absence from inception (*F. citrifolia*, *F. racemosa* and *F. religiosa*) or by abortion (*F. hispida*) in staminate flowers. The perianth is formed by a single whorl of sepals, as found in other families related to Moraceae. The gynoecium is tubular during development, a condition that may be related with pseudomonomery. The staminate and neutral flowers in *F. hispida* develop by similar mechanisms. The diversity in the sexual systems in *Ficus* results from combinations of different floral morphs (dicliny), which originate from both previously established ontogenetic mechanisms (loss of reproductive organ function by abortion or from inception). These mechanisms act independently of phylogenetic proximity or mechanisms of sex system evolution in *Ficus*. Other aspects of floral development observed in *Ficus* are discussed in relation to their systematic position and reproductive biology.

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1. Introduction

The absence of reproductive whorls in diclinous flowers (= unisexual flowers) can occur at any developmental stage (Diggle et al., 2011), and it is traditionally classified in two categories (Mitchell and Diggle, 2005). The most common includes flowers that underlie loss of reproductive organ function by aborting the stamens or carpel at any developmental stage of floral development. In the other type, only carpel or stamen primordia are formed, with no rudiment or remnant of the other whorl being observed. However, the relation between ontogenetic process and sexual system has been poorly explored (Diggle et al., 2011), especially among different members within a taxonomic group.

Ficus L. (Moraceae) is an interesting model for floral developmental studies because of its remarkable floral features, unexplored in terms of ontogeny, and the diversity of the sexual systems found within this species-rich genus of angiosperms. *Ficus* has urn-shaped inflorescence called syconium (Datwyler and Weiblen, 2004; Clement and Weiblen, 2009), which coevolved through obligate mutualism with pollinating agaonid wasps (Cook and Rasplus, 2003; Kjellberg et al., 2005; Cruaud et al., 2012). The syconium, or fig, represents an urceolate receptacle (Weberling, 1989) that typically encloses diclinous flowers (Berg, 1990). Pollinating wasps enter into the syconium through the ostiole (Galil and Eisikowitch, 1968), which is formed by bracts arranged spirally or in multiple series, pollinate pistillate flowers and lay eggs in some of the ovaries (Berg, 1990; Berg and Corner, 2005). Therefore, fig trees and agaonid wasps rely on each other for sexual reproduction.

Approximately half of the ca. 750 *Ficus* species are monoecious (Berg, 1989a). Syconia of monoecious species enclose pistillate and staminate flowers, where pollen, seeds and wasp galls are produced (Cook and Rasplus, 2003; Weiblen, 2004). The other species are structurally gynodioecious but functionally dioecious (Berg and Corner, 2005). Gynodioecious species include (a) individuals with
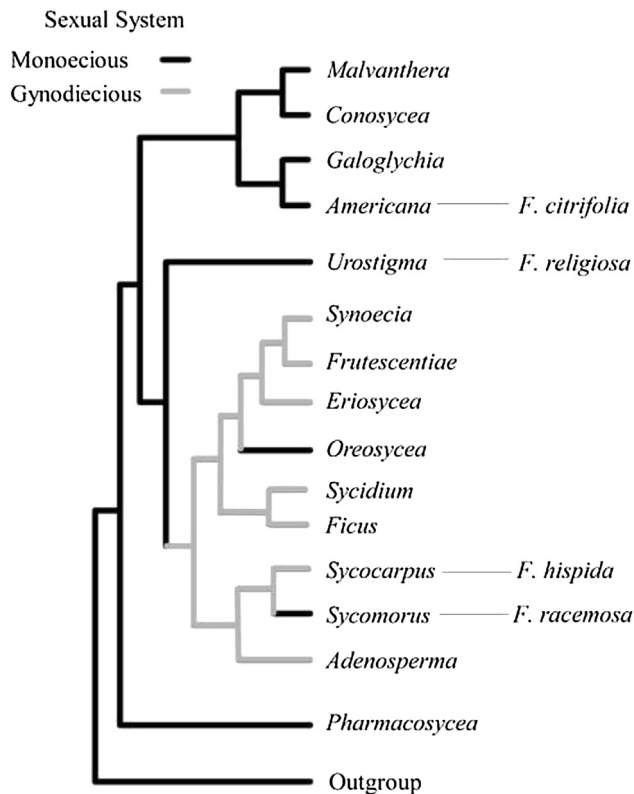
Sexual System

Monoecious ▬▬
Gynodiecious ▬▬

Fig. 1. *Ficus* phylogeny. Relationships between sections of the genus. Gynodioecy appears in *Ficus* from ancestral monoecy, but reversion to the ancestral state occurred in section *Sycomorus* and *Oreosycea*. Phylogeny modified from Cruaud et al. (2012).

syconia containing exclusively pistillate flowers and (b) individuals with syconia containing pistillate and staminate flowers (Kjellberg et al., 1987). For simplicity, these plants will hereafter be referred to as "female trees" and "male trees", respectively. Syconia of female trees have long-styled pistillate flowers that are inaccessible to wasp oviposition. Thus, these syconia produce only seeds (female function) (Verkerke, 1987) because, although agaonid wasps pollinate the flowers, they are not able to lay eggs. Conversely, syconia of male trees have short-styled pistillate flowers, and pollinators have access to all pistillate flowers for oviposition. Therefore, although bearing pistillate flowers, syconia of male trees produce only wasp offspring and pollen (male function) (Cook and Rasplus, 2003).

However, each type of sexual system has a distinctive phylogenetic history among the *Ficus* lineages. Monoecy seems

to be the ancestral character-state in the genus, with one (or more) change to gynodioecy (Weiblen, 2000; Jousselin et al., 2003a; Datwyler and Weiblen, 2004) (Fig. 1). At least two reversals to monoecy seemed to occur in the gynodioecious group (e.g. section *Sycomorus*), considered here as secondarily monoecious and structurally identical to the ancestral monoecy (Weiblen, 2000). The lability in these features raises questions on which ontogenetic pathways promote such phenotypic plasticity in the genus.

To assess the ontogenetic pathways that promote diclinous flowers in *Ficus*, we compared the morphology of flowers across development for four species representing independent lineages (Cruaud et al., 2012) with different sexual systems: *Ficus citrifolia* (monoecious, section *Americana*), *Ficus religiosa* (monoecious, section *Urostigma*), *Ficus racemosa* (secondarily monoecious, section *Sycomorus*), and *Ficus hispida* (gynodioecious, section *Sycocarpus*). In addition, aspects of floral development are discussed in relation to the systematic position and the reproductive biology of the group.

2. Material and methods

Species were selected for this study based on their sexual expression (Table 1) (Galil and Snitzer-Pasternak, 1970; Pereira et al., 2000; Yang et al., 2002; Wang et al., 2005), and species were limited to include only those that are actively pollinated, to eliminate morphological variation that is associated with passive or active modes of pollination in the genus (see Jousselin and Kjellberg, 2001; Jousselin et al., 2004).

Syconia of different developmental stages were collected and were fixed in FAA 50 (formalin, acetic acid, alcohol) for 24 h (Johansen, 1940). Scanning electron microscopy (SEM) was used for the surface analyses. Dissected specimens were dehydrated in an ethanol series, critical-point dried with liquid CO_2 in a Bal Tec CPD 030, mounted on aluminum stubs with colloidal carbon, and coated with gold in a Bal Tec SCD 050 sputter-coater for 200 s. The samples were observed and illustrated with Shimadzu SS-550 and JEOL JSM 5200 scanning electron microscopes at 15–20 kV.

Light microscopy (LM) was used for anatomical analyses. Samples were gradually dehydrated in an ethanol series, embedded in glycol methacrylate resin (Leica historesin), sectioned transversely and longitudinally using a Leica RM 2245 rotary microtome (sections were at most 5 μm thick), and stained with 0.05% toluidine blue (O'Brien et al., 1964). The anatomical sections were observed and photographed under a light microscope (Leica DM 4500 B) coupled to a digital camera (Leica DFC 320).

Bracts associated with the ostiolar aperture are called orobracts (Mello-Filho et al., 2001) and the others associated with flowers are

Table 1
Information about the *Ficus* species selected for this study.

Species	Subgenus/Section	Sexual system	Collection site	Accession numbers
F. citrifolia Mill.	*Urostigma/Americana*[a]	Monoecious[c]	USP campus, Ribeirão Preto, Brazil	J.P. Basso-Alves 18 (SPFR)
F. religiosa L.	*Urostigma/Urostigma*[b]	Monoecious[d]	Rio de Janeiro Botanical Garden, Rio de Janeiro, Brazil Xishuangbanna Tropical Botanical Garden, Yunnan, China	M.F.C. Costa et al. 74 (SPFR) s/coll (HITBC 058160)
F. racemosa L.	*Sycomorus/Sycomorus*[b]	Secondarily Monoecious[e, f]	Rio de Janeiro Botanical Garden, Rio de Janeiro, Brazil Xishuangbanna Tropical Botanical Garden, Yunnan, China	s/coll (RB 422367) s/coll (HITBC 023212)
F. hispida L.	*Sycomorus/Sycocarpus*[b]	Gynodioecious[g]	Xishuangbanna Tropical Botanical Garden, Yunnan, China	s/coll (HITBC 023038)

[a] Carauta and Diaz 2002;
[b] Berg and Corner 2005,
[c] Pereira et al., 2000,
[d] Galil and Snitzer-Pasternak 1970,
[e] Wang et al., 2005,
[f] Weiblen 2000,
[g] Yang et al., 2002.

Table 2
Major differences in floral morphology observed among the *Ficus* species in this study.

Species	Extrafloral phyllome number per flower	Sepal number and union (pistillate flower)	Sepal number and union (staminate flower)	Stamen number	Stigma Morphology	Synstigma arrangement
F. citrifolia	1 (pistillate flower) 2 (staminate flower)	3 (united in long-styled flower) 3 (free in short-styled flower)	2 (united at the base)	1	Filiform (elongated papillae)	3–5 weakly aggregated stigmas
F. religiosa	2 (pistillate flower) 1 (staminate flower)	4–5 (free)	3 (free)	1	Filiform (elongated papillae)	Cohesive and continuous
F. racemosa	2 (staminate flower)	3–4 (united at the base)	4 (united at the base)	2	Clavate (short papillae)	Cohesive (by secretion) and continuous
F. hispida (female tree)	2 (neuter flower)	3 (united)			Infundibuliform (short papillae)	Cohesive and continuous
F. hispida (male tree)	2 (staminate flower)	3 (united)	4 (united)	1	Tubular (no papillae)	Absent

called simply "phyllomes" (Briggs and Johnson, 1979), due to uncertainty of arrangement of these elements in such a complex inflorescence (Verkerke, 1988). The adaxial/abaxial inflorescence axis was standardized according to the central axis or ostiole. Descriptions of floral morphology follow the guidelines proposed by Berg (1990).

3. Results

The studied species show variation both in floral organization and in patterns of floral distribution inside the syconium (Fig. 2). Pistillate flowers are abundant in all species, whereas staminate flowers are generally restricted to the ostiole region. The single exception is *F. citrifolia* in which staminate flowers are scattered into the syconium. All flowers are associate with phyllomes (typically one phyllome for pistillate flowers and two for staminate flowers), but none for the pistillate flowers of *F. hispida* and

F. racemosa. Sexual expression explains most of the variation in floral organization. In the monoecious species (*F. citrifolia*, *F. religiosa* and *F. racemosa*), pistillate and staminate flowers exist within the same syconium. The flowers are densely packed during the receptive phase of the stigma. The ovaries of the pistillate flowers form several layers inside the syconium, due to variation in style and pedicel lengths. In the gynodioecious *F. hispida,* there is a clear separation of floral morphs between syconia. The syconia of female trees have pistillate, long-styled flowers and a few neuter flowers that are restricted to the ostiole region. The syconia of male trees have pistillate, short-styled flowers and some staminate flowers in the ostiole region.

3.1. Ficus citrifolia (monoecious)

The syconium begins its development as a discoid receptacle and gradually assumes a globular shape through growth at its rims.
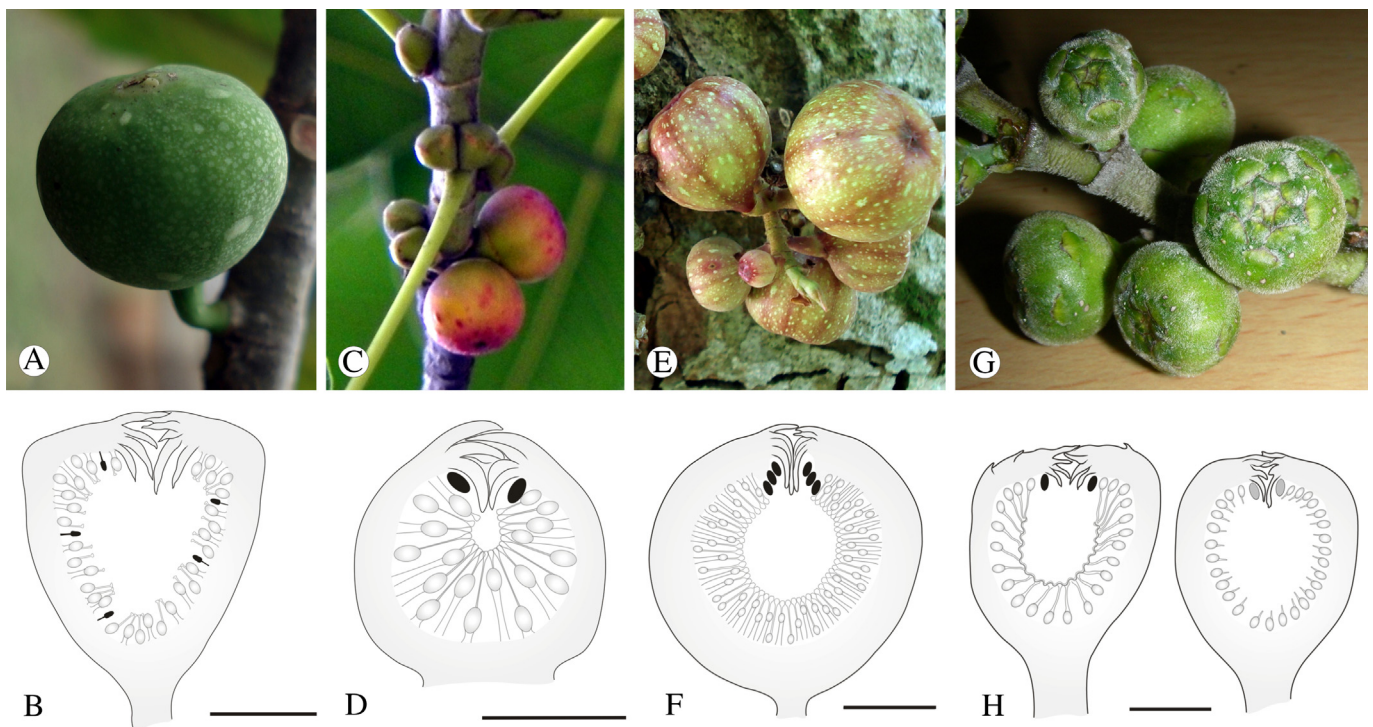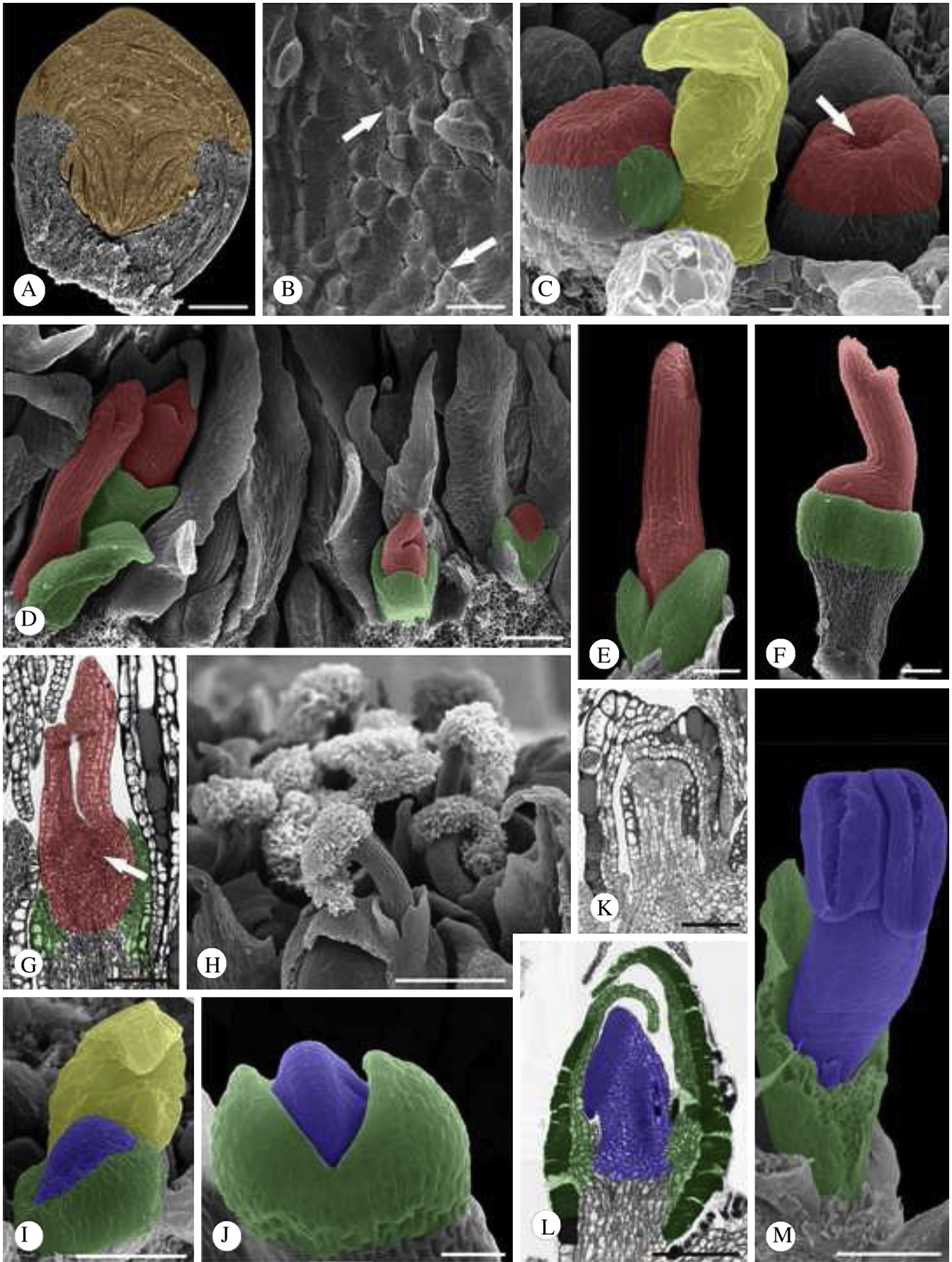

Fig. 2. Photographs and diagrams of *Ficus* syconia. (A, B) *F. citrifolia*. (C, D) *F. religiosa*. (E, F) *F. racemosa*. (G, H) *F. hispida* (left: syconium of a female tree, right: syconium of a male tree). Staminate flowers are shaded in black, and neuter flowers are shaded in grey. Scale bars = 1 cm.

The orobracts grow toward the syconium centre and fill the newly formed cavity (Fig. 3A). The first flowers arise in the gap created by the absence of orobracts, followed by additional young flowers, which emerge throughout the syconium (Fig. 3B). Two floral morphs - pistillate and staminate - develop from their respective floral primordia, which are similar at this developmental stage.

The young pistillate flower arises in association with a phyllome. The three sepals form in sequential order, immediately followed by the pistil (Fig. 3C). At this early stage, the pistil is cylindrical and more elongated than the sepals. The rim of the pistil becomes more prominent resulting in a tubular structure (Fig. 3C), with an oblique aperture. The development of pistillate flowers is asynchronous; therefore, flowers at several development stages are found side by side (Fig. 3D). Elongation of the pedicels is not uniform (Fig. 3E and F), positioning the developing ovaries at different heights inside the syconium. The style also extends heterogeneously and shows the most prominent elongation in sessile flowers (Fig. 3E). A single ovule forms inside the ovary before the carpel cleft closes (Fig. 3G). At this stage, the stigma begins to differentiate (Fig. 3D—F), and the sepals overgrow and cover the ovary. The final stage of pistillate floral development is marked by the presence of a flower with a uniovulate ovary, a glabrous lateral style, and a filiform stigma. The stigmatic surface has a perpendicular curvature in relation to the style, and it is composed of elongated papillae (Fig. 3H). Because the styles and pedicels are of different lengths, the stigmas of all of the flowers reach the same height in the lumen of the syconium. The sepals are usually lanceolate and free in sessile flowers but are fused into a tubular calyx in long-pedicelled flowers (Fig. 3E and F). Thus, the pistillate flowers exhibit gradual polymorphism. Three to five stigmas of adjacent flowers compose a weakly cohesive synstigma (Fig. 3H).

The young staminate flower is associated with two phyllomes and assumes a conical shape (Fig. 3I). The perianth organs appear as two opposite structures, which become united at the base (Fig. 3J). Only one stamen is formed, and the anther with the sporogenous tissue differentiates early (Fig. 3K and L). The sepals cover the young stamen at pistillate flower maturity. After this, filament elongation occurs through anticlinal cell divisions (especially in the adaxial side) and promotes anther exposition above the tubular calyx. The anther becomes perpendicular to the floral axis and then releases pollen in monads by longitudinal dehiscence (Fig. 3M).

3.2. Ficus religiosa (monoecious)

The first flowers arise in a discoid syconium (Fig. 4A). Orobracts grow and occupy the syconium cavity, exerting pressure on the syconium surface. Two floral morphs develop in the same syconium: pistillate and staminate.

The young pistillate flower is associated with two phyllomes, and forms four or five sepals and one pistil. The developing sepals and pistil elongate similarly (Fig. 4B and C), but elongation varies among the sepals (Fig. 4D). The developing pistil has a tubular

shape and oblique aperture (Fig. 4D). A single ovule forms before the closure of the carpel cleft (Fig. 4C). Differences between pedicel lengths occur during style elongation and are most evident in the adaxial region of the syconium (Fig. 4E and F). The pistillate flowers are compactly arranged. The ovaries occupy different heights inside the syconium (Fig. 4G), due to pedicel length variation. The perianth consists of 4—5 lanceolate sepals. The style is glabrous and shows a wide range of lengths, although the stigmas always reach the same level in the syconium. The stigma is filiform and composed of intertwined elongated papillae; together with other stigmas, they form a cohesive synstigma (Fig. 4H).

The young staminate flower is associated with one phyllome, and initiates three sepals and one stamen (Fig. 4I). The developing sepals grow fast and cover the conical stamen at anthesis (Fig. 4J). The staminate flower is sessile and has free sepals and a sessile stamen (Fig. 4K). The anther dehisces longitudinally, and the filament has elongated trichomes at its base (Fig. 4L).

3.3. Ficus racemosa (secondarily monoecious)

The first floral apices arise sparsely (Fig. 5A) in a globular syconium. The orobracts are restricted to the ostiole at this stage, and they partially occupy the lumen of the syconium. Two floral morphs develop: pistillate and staminate.

The emergence of pistillate flowers is asynchronous, resulting in flowers at several stages of development side by side. No phyllome is present. Three or four sepals arise, immediately followed by the formation of the pistil (Fig. 5B). Elongation of the developing pistil is more accentuated than that of the sepals. The young pistil is cylindrical and its rim grows as a tube (Fig. 5B). Only one ovule develops (Fig. 5C). Larger floral apices develop longer pedicels. The wide space on the receptacle surface formed between the pistillate flowers during development is occupied by trichomes. The sepals become almost completely united, but retain 3—4 free lobes. Asynchrony in the stages of floral development occurs within a single syconium (Fig. 5D). Differentiation of the stigma begins in young flowers located on the adaxial side of the syconium. Later in development, the tubular calyx encloses the ovary. The ovaries are ellipsoidal and smooth, and they are positioned at different heights inside the lumen of the syconium (Fig. 5E). The styles are glabrous and vary in length. The floral packaging is accentuated at maturity (Fig. 5E). The stigma is clavate, has a shallow central depression, and is composed of short papillae. A cohesive synstigma is formed by the union of all stigmas through an abundant exudate and the mechanical coherence of short papillae (Fig. 5F).

The young staminate flower is larger than the pistillate one (Fig. 5G). It is associated with two phyllomes laterally and becomes ellipsoidal (Fig. 5H). It initiates four sepals, followed by a central stamen (Fig. 5I and J). The phyllomes assume a hooded shape and completely cover the floral bud until anthesis. The terminal stamen primordium becomes ellipsoidal and divides into two stamens (Fig. 5K). The abaxial sepal elongates more than the other sepals, although all of them are united at the base (Fig. 5K and L). The

Fig. 3. Floral development of the monoecious *Ficus citrifolia*. (A) Early stage of syconium development (SEM). (B) Emergence of floral apices (arrows) inside the syconium, first emerging in regions of lower pressure exerted by the orobracts (SEM). (C) Two young pistillate flowers. Extrafloral phyllome and sepals are seen in the floral bud on the left, and a developing pistil with a prominent rim (arrow) is seen on the right (SEM). (D) Overview of the syconium inner surface, showing the asynchronous development of pistillate flowers and extrafloral phyllomes. Note the pistillate flowers in both early (right) and late (left) stages of development (SEM). (E) Pistil elongation in a sessile floral bud (SEM). (F) Sepals are united in a short-styled pistillate flower (SEM). (G) Ovule initiation (arrow) in the open pistil. Observe the stigmatic differentiation (LM). (H) Pistillate flowers arranged at the same level inside the syconium. Note that some stigmas remain close to each other. (I) Elongation of two phyllomes and initiation of two sepals and one stamen in a staminate flower (SEM). (J) Developing perianth partially enclosing the developing stamen (SEM). (K) Longitudinal section at a stage similar to that shown in J. Note the differentiation of sporogenous tissue (ML). (L) Young stamen with sporogenous tissue and filament elongation (SEM). (M) Staminate flower at anthesis, showing longitudinal dehiscence and elevated anther. Artificial colours: yellow = phyllome, orange = orobracts, green = perianth, blue = stamen, red = pistil. Scale bars = 200 μm (A), 50 μm (B, E, I, J), 10 μm (C), 100 μm (D, F, G, K, L), 500 μm (H, M). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
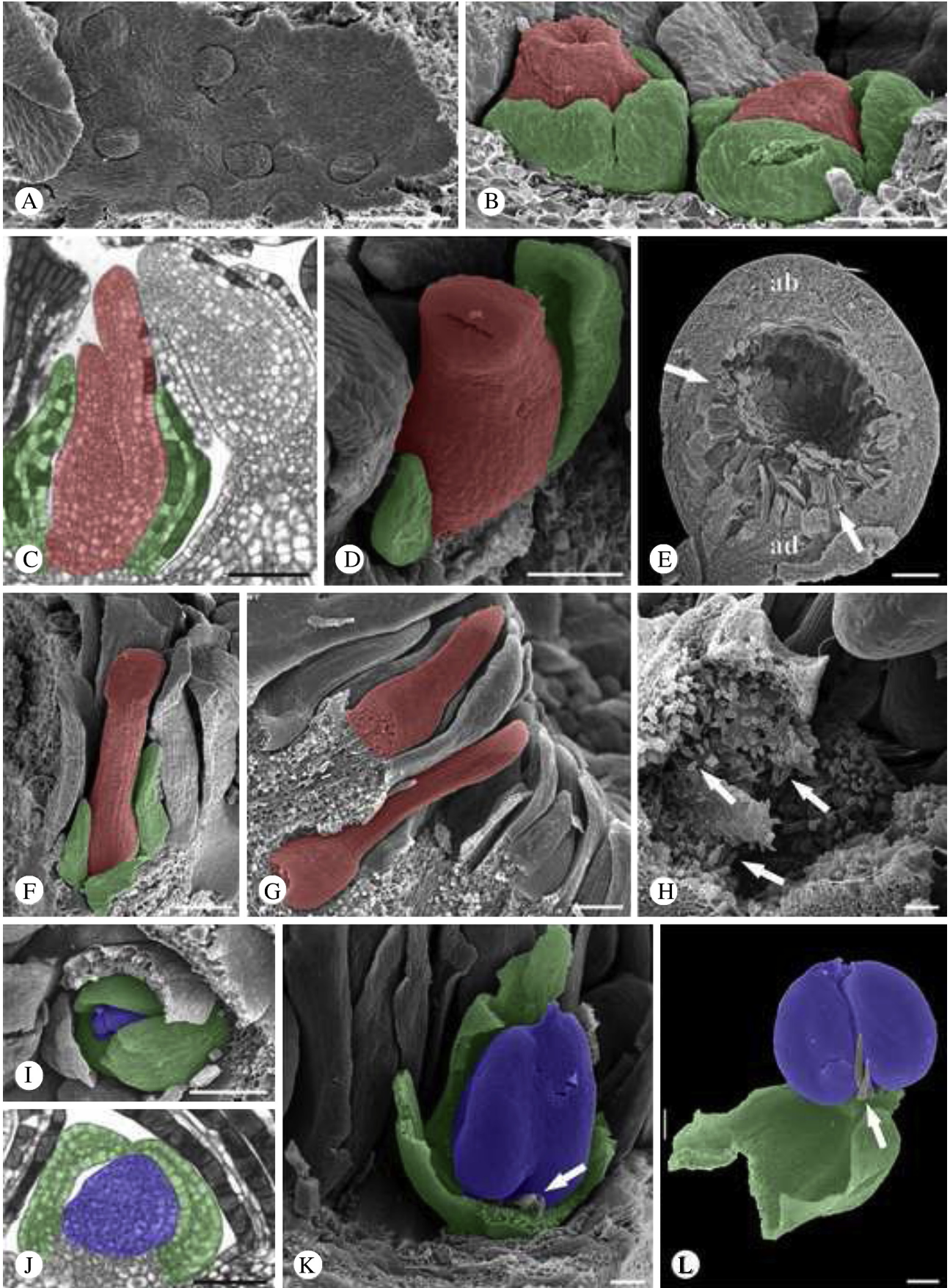
stamens are introrse and the filaments remain united at the base. Staminate flowers have a tubular calyx with four apical lobes and two stamens (Fig. 5M). The anthers are exposed by the elongation of the filaments, and dehiscence is longitudinal.

3.4. Ficus hispida (gynodioecious)

The early stages of syconium development are identical in both syconium types. After adopting a discoid shape, the syconium becomes globular, with orobracts pressing on only the syconium border. The young flowers emerge sparsely (Fig. 6A), and the syconium cavity expands, increasing the space between the developing flowers (Fig. 6B). Four floral morphs develop: short-styled pistillate, long-styled pistillate, staminate and neuter.

The young pistillate flower initiates three sepals, followed by the central pistil (Fig. 6C). The sepals are united forming a ring around the pistil (Fig. 6D). The developing pistil becomes tubular (Fig. 6E). The single ovule begins developing before the carpel cleft has closed (Fig. 6F). All of the pistillate flowers are sessile, no phyllomes are present, and their ovaries are located at the same level inside the lumen of the syconium (Fig. 6G and H). Differences occur in the sepal, style and stigma of each syconium type (e.g., male and female trees). In the syconium of a female tree, the sepals form a ring at the base of the ovary, the style has long trichomes, and the stigma is funnel-shaped and has short papillae (Fig. 6G). In the syconium of a male tree, the sepals completely cover the ovary, the style is glabrous, and no papillae occur in the stigma (Fig. 6H). Style lengths are uniform within each type of syconium, although the syconia of female trees have longer styles than the syconia of male trees. A cohesive synstigma is present in the syconia of female trees (Fig. 6I and J), while stigmas in the syconia of male trees do not maintain contact with each other (Fig. 6H).

Young staminate flowers are found only in the syconia of male trees, arranged in one or two rows around the syconium ostiole. Two phyllomes develop laterally (Fig. 6K), followed by four sepals, one stamen, and an organ arrested in development on the abaxial side (Fig. 6L and M). This arrested organ seems to be a pistil, not a stamen, taking into account that staminate flowers of other species included in sect. Sycocarpus have only one stamen (see Berg and Corner, 2005). Thus, the pistil is aborted early, while the stamen proceeds in its development (Fig. 6M).

The young neuter flowers are associated with two lateral phyllomes, and form four sepals (Fig. 6N) and one central primordium. The central primordium does not differentiate morphologically and does not develop any sporogenous tissue (Fig. 6O). Perianth development is similar to that of staminate flowers.

4. Discussion

4.1. Diclinous flowers and sexual expression

Dicliny in Ficus is promoted by (1) stamen absence from inception in pistillate flowers and (2) pistil absence from inception (F. citrifolia, F. religiosa and F. racemosa) or by abortion (F. hispida) in staminate flowers. Thus, sexual expression (monoecy, gynodioecy) in this group is defined by the combination of different ontogenetic processes and is independent of the Ficus lineage.

In Moraceae, absence of pistils from inception is common in monoecious species, while staminate flowers with aborted pistil are more common in gynodioecious/dioecious species (see Table 3). However, exceptions do occur. Ficus sycomorus, for example, is a monoecious species that exhibits aborted pistil, while Maclura pomifera, a dioecious species, exhibits pistil absence from inception. Furthermore, the presence of pistillodes, identifying pistil abortion, has been mentioned in monoecious species belonging to the sections Pharmacosycea and Sycomorus (Corner, 1981; Berg, 2001; Berg and Corner, 2005), suggesting that pistil abortion may be more frequent than the pattern observed here might suggest. It is also possible that aborted pistil (presence of pistillodes) might represent a character state that is maintained across lineages, with pistil absence from inception (no pistillodes found) occurring in other lineages, such as Urostigma and Americana (see Fig. 1).

Compared to other angiosperms, and similar to other Moraceae species and related plant families (Ronse De Craene, 2010), floral organization is quite simple in Ficus. An important feature of the urticalean rosids is the tendency toward floral reduction (Berg, 1977, 1989b), expressed in dicliny (Ronse De Craene, 2010), apetaly (Ronse De Craene, 2003; Endress and Matthews, 2006), hypanthium loss in relation to other Rosales (Ronse De Craene, 2010), and pseudomonomery (Bechtel, 1921; Eckardt, 1937). Floral reduction in Moraceae seems to be accompanied by changes in the organization of the inflorescence, resulting in compact and complex architectures (Berg, 1977, 1989b, 2001; Datwyler and Weiblen, 2004; Ribeiro, 2007; Clement and Weiblen, 2009; Endress, 2010), as also seen, e.g., in Euphorbiaceae (cyathium; Prenner and Rudall, 2007), Hydatellaceae (pseudanthium; Rudall et al., 2009) and Betulaceae (cymule; Lin et al., 2010).

4.2. Floral morphs

The pistillate flower is the most abundant floral type in actively pollinated Ficus species (∼90%; Berg, 1990). Each organ is coordinated with the whole (Schlichting and Pigliucci, 1998) maintaining internal organization of the syconium during development. The syconium (Verkerke, 1988) severely limits the space available for the early development of non-functional organs, especially in syconia with compact floral arrangement of monoecious species such as F. citrifolia and F. religiosa. Thus, stamen absence from inception could be a result of syconium organization in response to these ontogenetic and mechanic constraints (Datwyler and Weiblen, 2004; Clement and Weiblen, 2009). Because stamen absence from inception is widely found in Moraceae (see Table 3), which also has complex inflorescence architectures (Berg, 1977, 2001; Clement and Weiblen, 2009), this condition should be found in the basal clades of the family.

The position of staminate flowers within the syconium does not depend on sexual expression in Ficus. F. citrifolia was the only

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Fig. 4. Floral development of the monoecious Ficus religiosa. (A) Early stages of syconium development, during the emergence of the first floral apices (SEM). (B) Two pistillate flowers at different developmental stages, the flower on the left showing the tubular pistil, and the flower on the right showing sepals of similar lengths (SEM). (C) Longitudinal section of a developing pistillate flower showing an open pistil (LM). (D) Pistillate flower at a similar stage to that shown in C with a tubular pistil and sepals of different lengths (SEM). (E) Syconium showing adaxial flowers that are more developed (arrow) than the abaxial ones (arrow) (SEM). (F) Pistillate flower during style elongation. (G) Pistillate flowers with conspicuous differences in pedicel/style lengths (SEM). (H) Several stigmas with elongated papillae (arrows) forming a cohesive synstigma (SEM). (I) Staminate flower in an early stage of development, composed of three sepals and one stamen. Note the single extrafloral phyllome (SEM). (J) Conical young stamen covered by two sepals at longitudinal section (LM). (K) Appearance of a staminate flower during pistillate flower anthesis (SEM). Note the trichomes (arrow) at the filament base. (L) Staminate flower in anthesis. Note the long trichomes (arrow) at the filament base and the longitudinal dehiscence of the anther (SEM). Symbols: ab = abaxial, ad = adaxial. Artificial colours: yellow = phyllome, green = perianth, blue = stamen, red = pistil. Scale bars = 100 μm (A, C, F, G, H, I, K, L), 50 μm (B, D, J), 500 μm (E). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
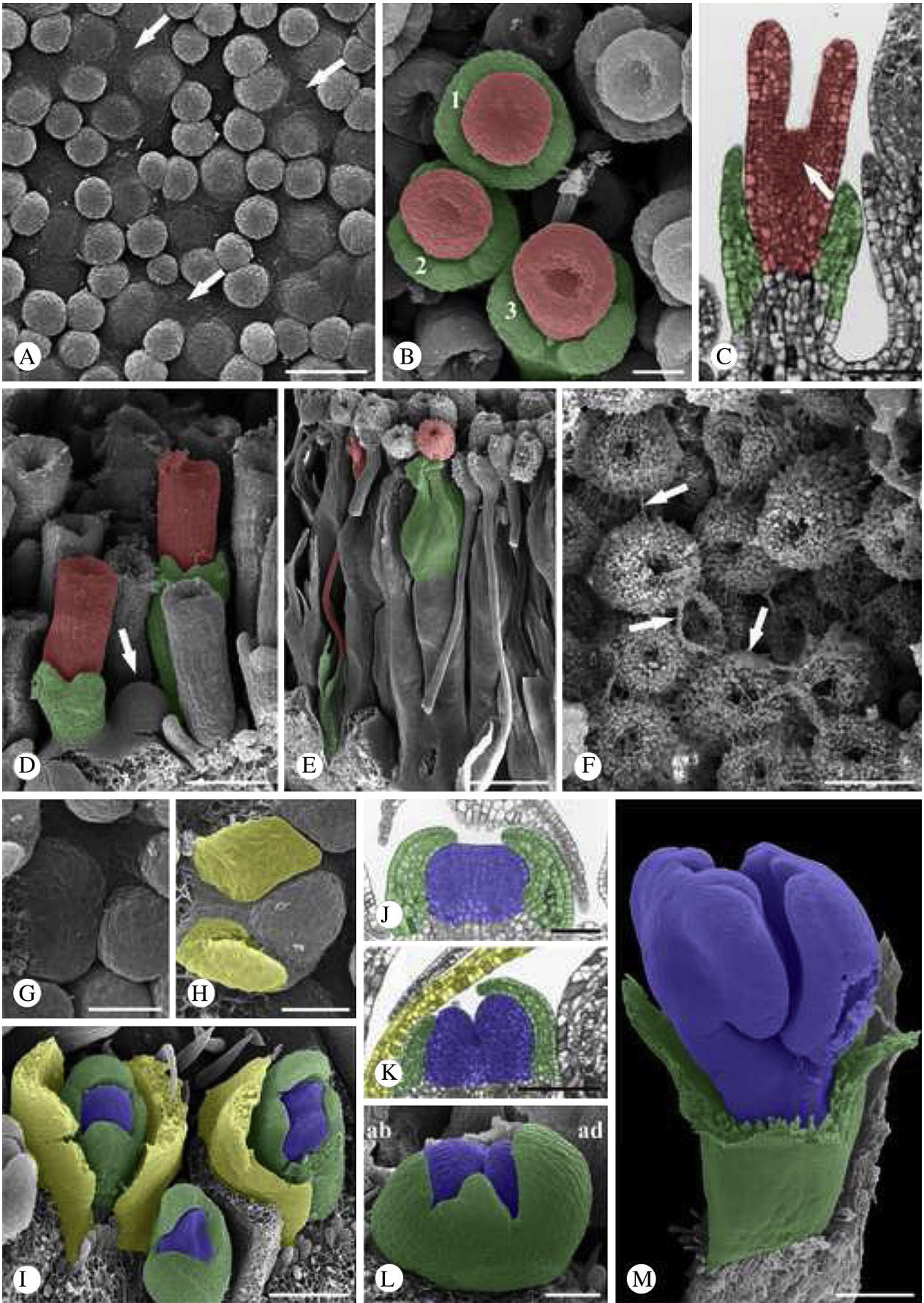
species with staminate flowers spread throughout the inflorescence, while in *F. religiosa, F. racemosa,* and *F. hispida*, staminate flowers are restricted to the area around the ostiole. Staminate flowers that are dispersed throughout the syconium are most commonly found in species of the sections *Americana* and *Galoglychia* and in species of the subgenera *Sycidium* and *Synoecia* that have reverted to passive pollination (F. Kjellberg, personal communication). This distribution pattern seems to be apomorphic within the genus, acquired several times from the ancestral condition "ostiolar staminate flowers". In ostiolar staminate flowers, orobracts impose intense pressure on the floral apex, which could be responsible for the pronounced protogyny reported in the genus (Verkerke, 1988; Berg, 1990).

The pistil abortion in staminate flowers of *F. hispida* (present study) may be considered precocious compared with that found in *F. sycomorus* (Galil and Snitzer-Pasternak, 1970) and *Ficus carica* (Beck and Lord, 1988). The young pistil in *F. sycomorus* and *F. carica* is aborted at the time the sporogenous tissue is formed, resulting in a vestigial organ or pistillode. Pistillodes may retain typical features of mature pistils (Verkerke, 1987; Berg, 2001) or they may have a very different structure, as in section *Pharmacosycea* (Berg and Corner, 2005). Pistillodes can occur in both monoecious (e.g., sections *Pharmacosycea* and *Sycomorus*) and gynodioecious groups (e.g., sections *Ficus, Kissosycea, Sycidium,* and *Sycocarpus*) (Berg and Corner, 2005). The functionality of the pistillode is controversial: in some cases, a pistillode may house a wasp gall (Berg, 1990), but in general, pistillodes do not have a particular role.

Ficus hispida and all other gynodioecious species of *Ficus* have neuter flowers (Berg and Corner, 2005). This floral type replaces staminate flowers in the syconia of female trees (Berg, 1990) and consists of a perianth and aborted stamens (Berg and Corner, 2005). The abortion of reproductive function in these flowers is more precocious in *F. hispida* (present study) than in *F. carica* (Beck and Lord, 1988). Neuter flowers are probably homologous to staminate flowers (sensu Hall, 2003; Rutishauser and Moline, 2005), considering their position within the syconium and the order of organ initiation in each whorl. These flowers must have lost their reproductive function during the transition from monoecy to gynodioecy in *Ficus*.

4.3. Remarkable developmental features of flowers

Certain developmental features of the gynoecium are remarkable in *Ficus*, such as pseudomonomery and the synstigma.

Despite the fact that the gynoecium seems to be composed of one carpel in *Ficus* (a single primordium was observed in *F. citrifolia, F. religiosa, F. racemosa,* and *F. hispida* in the present study; *Ficus asperifolia* in Verkerke, 1987; *F. carica* in Beck and Lord, 1988, 1988; and *Ficus sur* in Verkerke, 1988), the presence of two stigmatic branches in several species (Rohwer, 1993; Berg, 2001) and some studies of vascularization (Johri and Konar, 1956; Galil et al., 1970) both confirm the existence of a bicarpellar gynoecium in this group. In addition, a supplementary and

anomalous carpel was observed in *F. carica* (Payer, 1857) and *Ficus insipida* (Do Ó, 2008) and has been similarly observed in other urticalean rosids, including *Dorstenia* (Moraceae; Granville, 1971), *Morus nigra* (Moraceae; Payer, 1857), *Cannabis sativa* (Cannabaceae; Payer, 1857), *Celtis tournefortii* (Cannabaceae; Eckardt, 1937), *Humulus lupulus* (Cannabaceae; Shephard et al., 2000), and *Zelkova serrata* (Ulmaceae; Okamoto et al., 1992). As early as 1937, Eckardt had characterized the gynoecia of the Moraceae and other urticalean rosids as being pseudomonomerous (i.e., having a gynoecium composed of more than one carpel but with only one functional carpel, with the others being reduced - Ronse De Craene, 2010). However, considering the concept of pseudomonomery presented by Weberling (1989), emphasizing that the initiation of multiple carpels may be directly observed, there is carpel absence by abortion and not from inception. Therefore, the pseudomonomery is a very complex character state (González and Rudall, 2010) that needs urgent revision (Endress, 2011) to support its use in Rosales.

The presence of a synstigma in the actively pollinated species of *Ficus* (Jousselin and Kjellberg, 2001; Jousselin et al., 2003a; present study) is considered to be an adaptation for mutualism with pollinating wasps (Verkerke, 1989; Berg, 1990; Jousselin et al., 2003b). The synstigma functions as a common surface for pollen germination (Verkerke, 1989), allowing pollen tubes emitted by the pollen grains deposited on a flower to grow laterally and fertilize adjacent flowers (Verkerke, 1989; Jousselin and Kjellberg, 2001; Jousselin et al., 2003a). The synstigma of *Ficus* exhibits great diversity in terms of morphology and the degree of cohesion (see Table 2). However, further comparative studies are needed to clarify whether this structural diversity underlies functional differences.

4.4. Conclusions

The diversity of sexual expression in *Ficus* results from combinations of different floral morphs (diclinous flowers), originating from two previously established ontogenetic mechanisms - organ absence from inception or by abortion during floral development. These processes in *Ficus* occur independent of phylogenetic proximity or the mechanism of sex system evolution. Monoecy seems to be the ancestral character state in the genus, with at least one change to gynodioecy (Weiblen, 2000; Jousselin et al., 2003b; Datwyler and Weiblen, 2004) (Fig. 1). A reversal to monoecy seems to have occurred in one gynodioecious group (i.e., section *Sycomorus*). This reversal is considered here as secondary monoecy, and these plants are structurally identical to the ancestral monoecious state (Weiblen, 2000). Functional dioecy in *Ficus* is closely associated with both heterostyly (Berg, 1990) and the loss of reproductive function in staminate flowers (described here as neuter flowers). The origin, maintenance, and modification of this genetic system remain unclear (Weiblen, 2000), although the literature establishes that, in gynodioecious species, male trees are heterogametic (Parrish et al., 2004).

Fig. 5. Floral development of the secondarily monoecious *Ficus racemosa*. (A) Asynchronous emergence of floral apices within the syconium. Observe the gaps on the receptacle surface left between the flowers (arrows) (SEM). (B) Sepals and pistil of young pistillate flowers. The numbers indicate the developmental sequence of the pistil tube formation (SEM). (C) Longitudinal section of a floral bud showing ovule initiation (arrow) in an open pistil (LM). (D) Pistillate flowers showing different stages of organ elongation. The arrow indicates a floral apex without organ primordia (SEM). (E) Pistillate flowers at maturity, with ovaries occupying different levels inside the syconium, due to the variation in pedicel lengths (SEM). (F) Cohesive synstigma, united by an abundant exudate (arrows) and the mechanical coherence of short papillae (SEM). (G) Larger staminate floral apex (left) than a pistillate floral apex (right) (SEM). (H) A pair of young extrafloral phyllomes associated with a staminate floral apex (SEM). (I) Staminate flowers in successive stages of development (SEM). (J) Longitudinal section of a young stamen flanked by sepals (LM). (K) Longitudinal section of two basally united young stamens. Note the unequal length of sepals (LM). (L) Staminate floral bud during anther differentiation (SEM). ab = abaxial, ad = adaxial. (M) Staminate flower in pre-anthesis with two basally united stamens with intorse anthers (SEM). Artificial colours: yellow = phyllome, green = perianth, blue = stamen, red = pistil. Scale bars = 100 μm (A, D, I, K), 50 μm (B, C, G, H, J, L), 500 μm (E), 200 μm (F, M). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
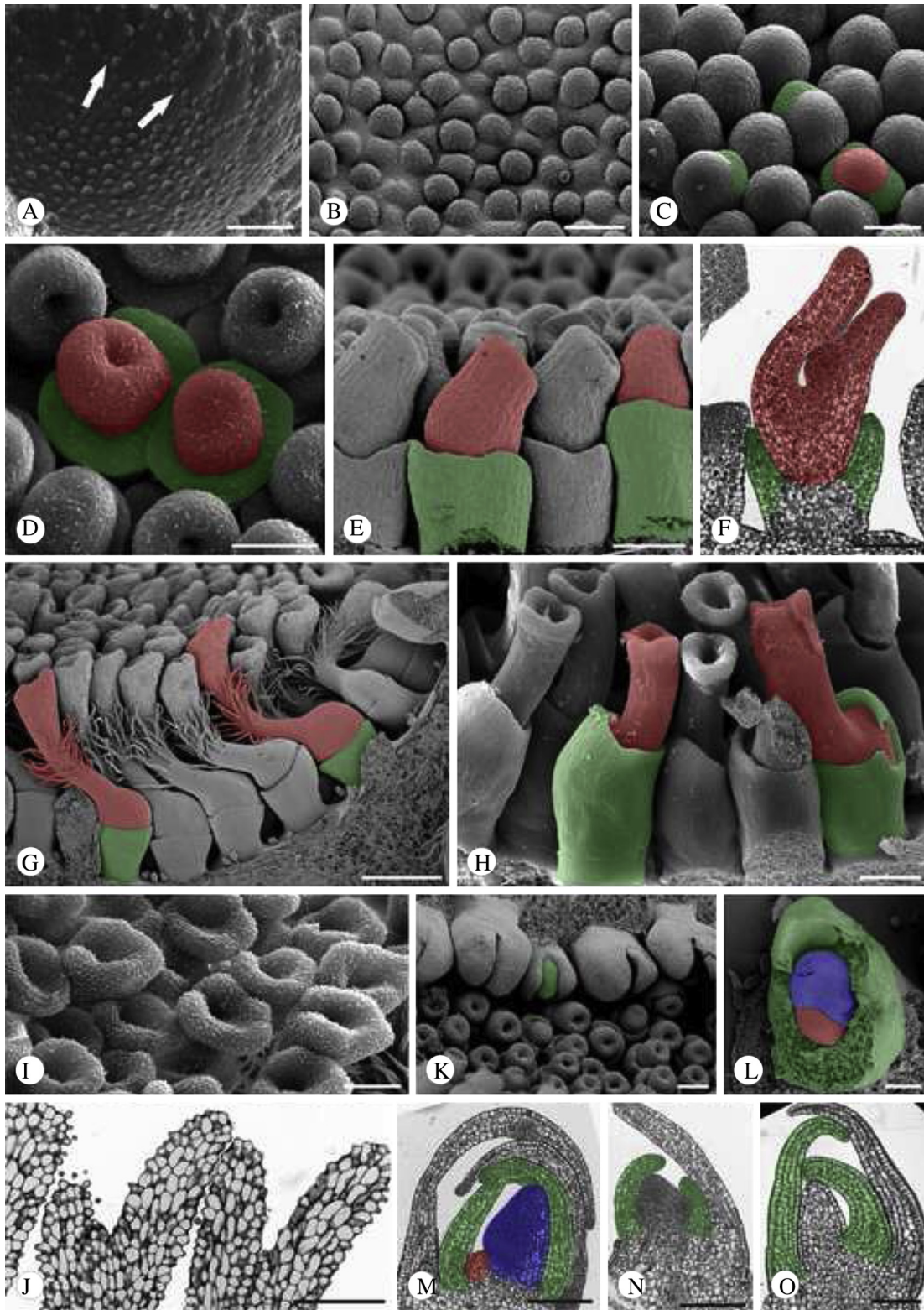
Fig. 6. Floral development of the gynodioecious *Ficus hispida*. Syconium of a female tree: D, E, F, G, I, J, N and O. Syconium of a male tree: A, B, C, H, K, L and M. (A) Floral apices are sparsely distributed in a young syconium and found around the gaps left by the orobracts (arrows) (SEM). (B) Floral apices in the adaxial region of syconium (SEM). (C) Sequential order of sepal initiation and a pistil primordium in young pistillate flowers (SEM). (D) Early stages of pistil development (SEM). (E) Tubular pistils during mid-development (SEM). (F) Longitudinal section of a developing pistillate flower showing ovule initiation in an open pistil (LM). (G) Pistillate flowers at anthesis, ovaries occupying the same level inside the lumen of the syconium. Note the hairy style (SEM). (H) Pistillate short-styled flowers at anthesis with the perianth completely surrounding the ovary (SEM). (I) Synstigma arrangement. (J) Synstigma in detail showing stigmas connected by short papillae (LM). (K) Buds of staminate (above) and pistillate (below) flowers (SEM). (L) Developing staminate flower with one stamen (adaxial) and one carpel (abaxial) (calyx partially removed) (SEM). (M) Longitudinal section of a similar stage to that shown in L, showing the sporogenous tissue and an aborted pistil primordium (LM). (N) Longitudinal section of a developing neuter flower, with a central primordium flanked by the perianth (LM). (O) Later stage of neuter flower development (LM). Artificial colours: green = perianth, blue = stamen, red = pistil. Scale bars = 200 μm (A), 100 μm (B, E, F, H, I, J, K, M, N, O), 50 μm (C, D, L), 500 μm (G). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Organ absence from inception (I) or by abortion (A) in reproductive whorls of some species of Moraceae, categorized according to sexual expression (D = dioecy, G = gynodioecy, M = monoecy). Empty cells indicate missing information.

Species	Tribe	Sexual system	Pistillate flower	Staminate flower	References
Artocarpus heterophyllus Lam.	Artocarpeae	M	I	I	Moncur 1985
Broussonetia papyrifera (L.) L'Hér. ex Vent.	Dorstenieae	D	I		Baillon 1861
Dorstenia astyanactis Aké Assi		M		A	Granville 1971
Dorstenia contrajerva L.		M		A	Granville 1971
Dorstenia embergeri Mangenot		M		A	Granville 1971
Dorstenia volkensii Engl.		M		A	Granville 1971
Ficus citrifolia Mill. (sect. *Americana*)	Ficeae	M	I	I	Present study
Ficus carica L. (sect. *Ficus*)		G	I	A	Condit 1932; Beck and Lord 1988
Ficus asperifolia Miq. (sect. *Sycidium*)		G	I	A	Verkerke 1987
Ficus hispida L. (sect. *Sycocarpus*)		G	I	A	Present study
Ficus racemosa L. (sect. *Sycomorus*)		M	I	I	Present study
Ficus sycomorus L. (sect. *Sycomorus*)		M	I	A	Galil et al., 1970
Ficus sur Forssk. (sect. *Sycomorus*)		M	I	I	Verkerke 1988
Ficus religiosa L. (sect. *Urostigma*)		M	I	I	Johri and Konar 1956, present study
Maclura pomifera (Raf.) C.K. Schneid.	Maclureae	D	I	I	Bechtel 1921, Maier et al., 1997
Morus alba L.	Moreae	D	I	A	Bechtel 1921
Morus nigra L.		D	I	A	Baillon 1861
Morus rubra L.		D	I	A	Maier et al., 1997

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