

FLORAL DEVELOPMENT IN THREE SPECIES OF *IMPATIENS* (BALSAMINACEAE)¹

PIETER L. CARIS,² KOEN P. GEUTEN, STEVEN B. JANSSENS, AND
ERIK F. SMETS

Laboratory of Plant Systematics, Institute of Botany and Microbiology, Katholieke Universiteit Leuven, Kasteelpark Arenberg 31,
B-3001 Leuven, Belgium

The floral morphological and developmental patterns in three species of *Impatiens* (Balsaminaceae), namely *I. columbaria*, *I. hawkeri*, and *I. niarniamensis*, were studied to contribute to a better understanding of floral evolution in the genus. Strangely enough, the highly diverse floral morphology and ontogeny of this horticulturally important genus have never been studied thoroughly (e.g., using scanning electron microscopic techniques). We discuss the position and the developmental sequence of the different perianth members. We hypothesized that in the course of evolution, the anterolateral sepals become reduced and that a morphocline can be recognized going from species with five sepals, over species with rudimentary sepals that fuse postgenitally with the anterior petal, to species where congenital fusion between these sepals and the anterior petal has taken place. Ovules generally are in one or two vertical rows per locule, but there are several vertical rows per locule in *I. columbaria*. The outer parts of the septa disintegrate to enable the explosive dehiscence of the capsules.

Key words: Balsaminaceae; Ericales; floral development; floral evolution; floral morphology; *Impatiens*; scanning electron microscopy.

The Balsaminaceae are a family of about 1000 species and two genera, the monotypic *Hydrocera* Blume and the large genus *Impatiens* L. (Fischer, 2004; Stevens, 2004). *Impatiens* is mainly distributed in the tropics and subtropics of the Old World, but several species occur in temperate Eurasia and North America. Native species are absent from South America and Australia. *Hydrocera* is a semiaquatic genus of the Indo-Malaysian region. Together with Marcgraviaceae and Tetrameristaceae s.l. (including *Pelliciera* Planch. & Triana), Balsaminaceae constitute the balsaminoid clade at the base of the Ericales (Anderberg et al., 2002; Bremer et al., 2002; Geuten et al., 2004). The monophyly of the Balsaminaceae and of the genus *Impatiens* itself are well supported (Yuan et al., 2004). *Hydrocera* can be characterized by its free petals and the berry-like capsular fruit, while *Impatiens* has four lateral petals connate in pairs and a five-valved, loculicid capsule. The sister-group relationship between *Hydrocera* and *Impatiens* is also confirmed by recent, molecular analyses (e.g., Yuan et al., 2004). Based on the overall morphology and distribution, several groups can be distinguished within *Impatiens*, but the relationships among these groups remain unresolved. The taxonomic difficulties are probably due to the existence of a large number of intermediate groups and taxa (Grey-Wilson, 1980a).

The often striking and beautifully colored flowers are hermaphroditic and are arranged in racemes, fascicles, or solitary in the axils of the leaves, or rarely pseudoterminally (Warburg and Reiche, 1895). Bracteoles are missing. In the African *Impatiens* species, all inflorescences can be considered to be variations of racemes, while species from the Himalaya are sometimes characterized by inflorescences without clear racemose organization (Akiyama and Ohba, 2000). For a detailed study

of the inflorescence types of *Impatiens*, we refer to Akiyama and Ohba (2000).

The flowers are resupinate, and consequently, the floral parts are often named according to the position they acquire after resupination. However, in our ontogenetic descriptions, we will refer to the original positions of the organs and use the terms abaxial and adaxial. In the discussion, we will speak about the posterior sepal, i.e., the lower, spurred sepal, the anterior petal on the opposite side, and according to the situation, the anterolateral or posterolateral sepals or petals (Fig. 1).

The zygomorphic flower (Fig. 1) is usually described as having three, or occasionally five sepals, of which the lower one (adaxial in origin) is much larger and often colored. Generally, it is characterized by a nectary-tipped spur (Fig. 1). On the inside of the apical part, the spur is lined with nectar-producing secretory cells. The corolla consists of five petals: a large and often partly sepaloid (i.e., green) one in the upper position (abaxial in origin), and four lateral ones, which are connate in pairs on the left and the right side of the flower (Fig. 1). The androecium has five stamens with short, broad filaments possessing partly fused and inwardly growing appendages at the top. The dithecal, tetrasporangiate anthers are connivent and open either apically or laterally by means of pores or slits. They lie as a cap above the gynoecium, which has a five-locular, syncarpous ovary and five stigmas. The style is very short or absent. Only after the pollen has been released and the androecium shed will the stigmas ripen. The coherent stigmas commonly spread and the star-shaped receptive surface is exposed. Hence, the flowers are protandrous, favoring cross-pollination. According to Takhtajan (1997), the stamens rupture at the base and are lifted by the gynoecium. The ovules are anatropous, bitegmic, and tenuinucellate, and they are arranged in one or two vertical rows on the axile placenta. The micropyle is directed upward and inward.

One of the best-known characteristics of *Impatiens* is the explosive dehiscence of the five-valved, loculicid capsule, resulting in the English names busy-lizzy and touch-me-not. The

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² Author for correspondence (e-mail: pieter.caris@bio.kuleuven.be)

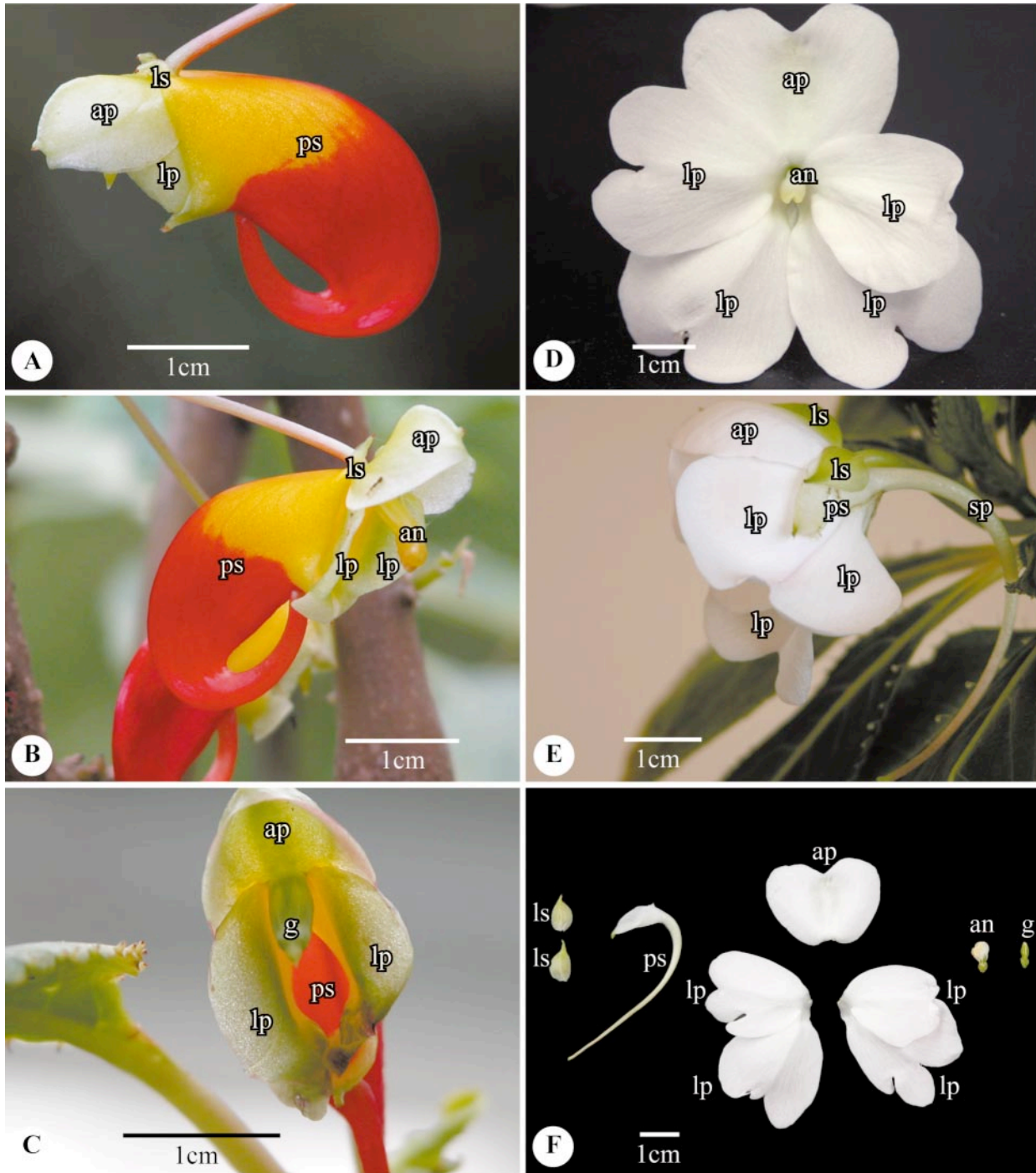


Fig. 1. A–C. *Impatiens niarniamensis*. A. Flower, lateral view. B. Flower, lateral view showing the androecium, which lies as a cap above the gynoecium. C. Flower, frontal view; the androecium is shed, exposing the gynoecium. D–F. *Impatiens hawkeri*. D. Flower, frontal view. E. Flower, lateral view. F. Floral parts of dissected flower. *Abbreviations*: *, top of the (inflorescence) axis; a, anther/stamen (primordium); ad, adaxial side of the flower; an, androecium; ap, anterior petal; b, bract; c, carpel (primordium); cn, connective; f, funicle; fi, filament; fp, flower primordium; g, gynoecium; lp, lateral petal; ls, lateral sepal; o, ovule (primordium); ov, ovary (wall); p, petal (primordium); ps, posterior sepal; s, sepal (primordium); sa, stamen appendage; se, septum; sl, style; sm, stigma; sp, sepal spur; v, vascular bundle.

valves of the fruit roll up inwardly and acropetally, which causes the seeds to be dispersed in all directions. What remains is the central axis of the fruit on which the seeds were attached, and at the top, the spirally winded valves. It may be clear that to effect such a dehiscence mechanism, a lot of ten-

sion has to be involved. Therefore, we paid special attention to the structure of the septa during our observations.

The floral morphology is highly diverse, and information on the developmental and evolutionary patterns within the genus is sparse (Yuan et al., 2004). The flowers are delicate struc-

tures, of which little remains in dried specimens. Therefore, herbarium material cannot be used to gain more insight on the morphology of the flower (Akiyama et al., 1991). The floral ontogeny has also been scarcely investigated, but studies like Payer (1857) help to illustrate the rich variety in the structure of the flower and may provide taxonomically useful characters.

The present study is part of a large study on floral development within Ericales, as defined by the Angiosperm Phylogeny Group (APG, 2003). We studied flowers and floral buds of three *Impatiens* species. We will first describe the overall ontogenetic pattern, using our observations on *I. niarniamensis* Gilg, a species of tropical West and Central Africa (Grey-Wilson, 1983). This frequently cultivated species is one of the most widespread, best-known, and most attractive species from Africa (Grey-Wilson, 1980a). Subsequently, we present our results from the poorly known *I. columbaria* J.J. Bos, a species with an initially pentamerous calyx and some interesting gynoeceum characteristics. It was discovered in 1985, and as far as we know, it can only be found in western Gabon (Grimshaw, 1998). Finally, we have studied the highly diverse *I. hawkeri* W. Bull, which was added here to illustrate the initiation and inner structure of the gynoeceum. It is distributed from New Guinea east to the Solomon Islands (Grey-Wilson, 1983). According to Grey-Wilson (1980b), the group around *I. hawkeri* forms a complicated and highly variable aggregate. Moreover, it has many cultivars that have become popular pot plants (Grey-Wilson, 1983).

These three species were selected because they encompass the basic variation in the flower morphology of the genus. Within *Impatiens*, two flower types can be distinguished on the basis of the spurred sepal (Grey-Wilson, 1980a). In the first type (represented here by *I. niarniamensis*; Fig. 1A–C), it has a funnel-shaped or saccate appearance and gradually continues into the spur. In the second type (represented by *I. hawkeri*; Fig. 1D) the spurred sepal is much smaller and it bears a filiform spur, which commonly is much longer than the sepal itself. *Impatiens columbaria* was added because this species possesses a pentamerous calyx, while the other two species are characterized by a trimerous calyx.

MATERIALS AND METHODS

The material of *I. niarniamensis* (voucher n°FB/S2590 and n°FB/S2642) and *I. columbaria* (voucher n°FB/S2966) was obtained from the greenhouse collection of the National Botanic Garden in Meise, Belgium. *Impatiens hawkeri* (voucher n°PCV06) was grown by the second author at the Laboratory of Plant Systematics, K.U.Leuven. Voucher specimens are kept at the National Botanic Garden in Meise and the Institute of Botany and Microbiology, K.U.Leuven.

The material was fixed in FAA (40% formalin, acetic acid, 70% alcohol, 5 : 5 : 90) and the floral buds were dissected in 70% ethanol under a stereomicroscope (Wild M3; Leica Microsystems AG, Wetzlar, Germany) equipped with a cold light source (Schott KL 1500; Schott-Fostec LLC, Auburn, New York, USA). To dry the material, the buds were washed twice for 5 min with 70% ethanol, for a further 5 min with a mixture (1 : 1) of 70% ethanol and DMM (dimethoxymethane), then the material was placed in pure DMM for 20 min. The samples were critical point dried using liquid CO₂ in a BAL-TEC CPD030 (BAL-TEC AG, Balzers, Liechtenstein). The material was mounted onto stubs using Leit-C and then gold-coated with a sputter coater (SPI Supplies, West Chester, Pennsylvania, USA). Observations were made using a JEOL JSM-5800 LV scanning electron microscope (JEOL Ltd., Tokyo, Japan) at the National Botanic Garden in Meise and a JEOL JSM-6360 microscope at the Laboratory of Plant Systematics, K.U.Leuven.

For the light microscopic observations, dehydrated floral buds of *Impatiens*

niarniamensis were embedded in Kulzer's Technovit 7100 (Kulzer Histo-Technik, Wehrheim, Germany). Serial sections, 5 µm thick, were stained with toluidine blue and mounted with Entellan (Merck, Darmstadt, Germany). Photographs were made using a Leitz Dialux 20 (Leica Microsystems AG, Wetzlar, Germany) equipped with an Olympus DP-50 digital camera (Olympus, Tokyo, Japan).

RESULTS

Impatiens niarniamensis Gilg—The flowers have long, slender pedicels and occur in clusters of two to six (to eight) in the axils of the leaves. The color of the flowers varies, but our material had red-yellow flowers: the spur is orange-red and the petals pale yellowish-green to whitish-green. The flower primordia arise spirally along the axis. They are initiated in the axil of a bract (Fig. 2A). Meanwhile, the first two sepal primordia are initiated on both sides of the flower primordium (Fig. 2B). Subsequently, the primordium of the large, spurred sepal originates at the adaxial side of the flower (Fig. 2C). Almost immediately afterward, another primordium becomes visible on the opposite side of the floral apex (Fig. 2D). This abaxially developing primordium will differentiate into the anterior petal. In the zone in between the large sepal and the anterior petal, the four remaining petal primordia arise in two successive pairs, the upper pair slightly before the lower pair (Fig. 2E). The petal primordia on the adaxial side, underneath the developing sepal, are somewhat smaller than the posterolateral petals (Fig. 2E). It is striking that in the development of the perianth, a clear distinction between the development of calyx and corolla is missing. The calyx arises in two stages, and the initiation of the anterior petal is intermediate with respect to the development of calyx and corolla (Fig. 2D–E). The four lateral petal primordia grow out independently, while the anterior petal always grows first (Fig. 2F). By common zonal growth at the base of the corolla, the petals fuse postgenitally (Fig. 2G). Next, five stamen primordia are initiated on an inner whorl, alternating with the corolla (Fig. 2H). They arise simultaneously, but due to differences in growth rate among the stamens, the androecium develops a zygomorphic appearance (Fig. 2I). The stamens on the abaxial side develop somewhat faster (Fig. 2I). While the developing stamens curve inward, the anthers have started to differentiate (Fig. 3A). The nearly triangular anthers are dithecal and tetrasporangiate; the connective has a papillose surface. During their development, the anthers become closely associated with each other and eventually are connivent (Figs. 3B, 4A). The sporangia of adjacent anther lobes will fuse before the pollen is released through a slit-like opening at the top of the anthers (Fig. 4A). On the floral apex, below the androecium, the gynoeceum is initiated (Fig. 3C). Five locules are defined by the inwardly growing septa, which fuse at the center only at the base (Fig. 3C). The ovary closes at the top, and five stigma lobes become apparent (Figs. 3D, 4B). The young gynoeceum as a whole has a barrel-like appearance, because a style seems to be lacking (Fig. 3D–E). The stigmas show little differentiation and can hardly be distinguished from the rest of the gynoeceum (Fig. 3E). In each of the five locules of the spindle-shaped, superior ovary, 10–15 unitegmic ovules develop; they are anatropous and possess a long funicle (Figs. 3F–K, 4C–E). The ovules within a locule are arranged in one vertical row (Fig. 4C) and develop in a basipetal order (Fig. 3F–H). Although they are all attached above each other (Figs. 3I, 4C), they will develop alternately to the left and to the right occupying the available

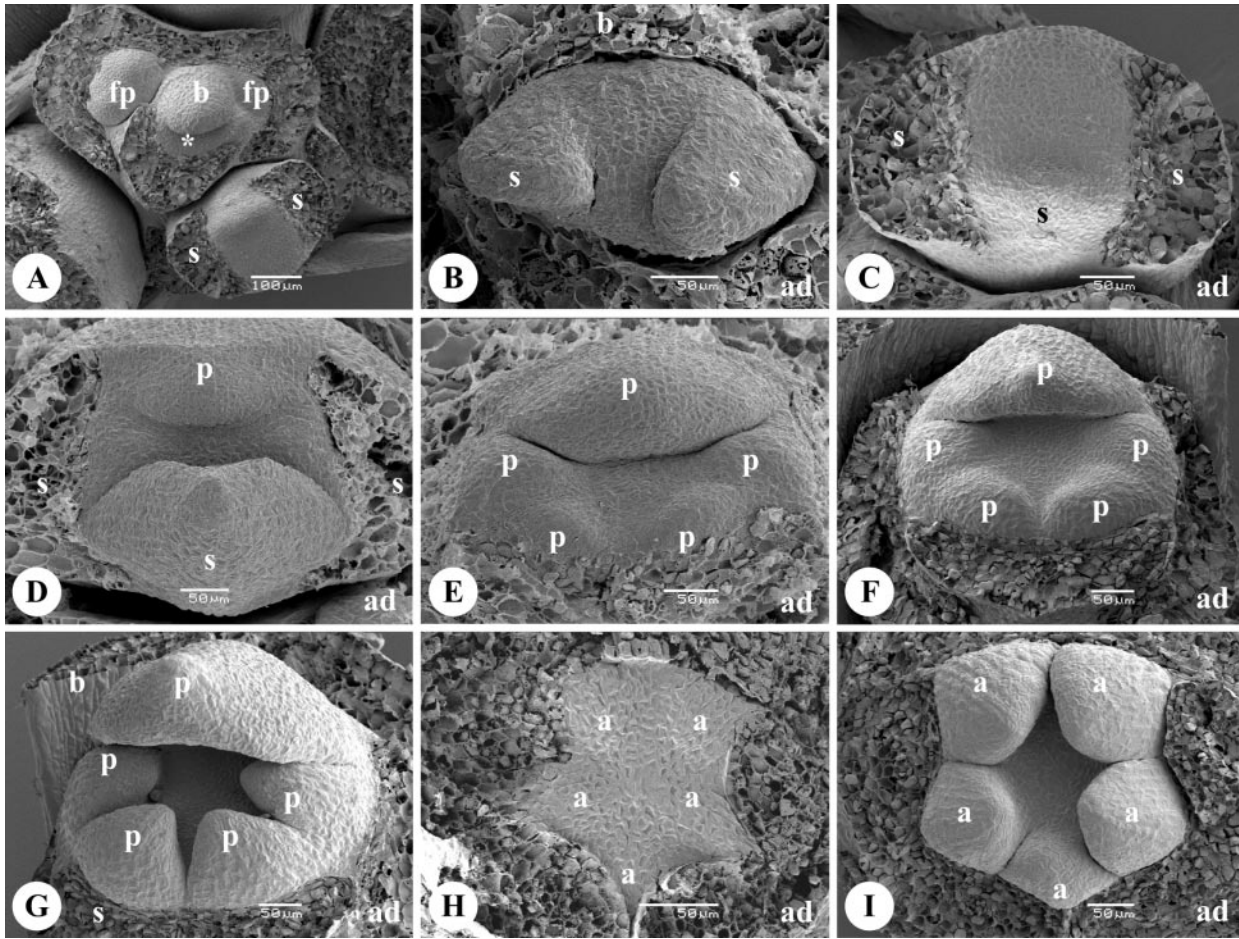


Fig. 2. Floral development of *Impatiens niarnniemensis*. **A.** Developing inflorescence: top view. **B.** Young flower primordium in axil of a bract with formation of the lateral sepals. **C.** Initiation of the adaxial sepal; the lateral sepals are removed. **D.** Initiation of the anterior petal in abaxial position (top of the picture), opposite the adaxial sepal. **E.** Origin of the lateral petals. **F.** Development of the petal primordia. **G.** The lateral petals have a triangular shape and curve inward. **H.** Five stamens at the same stage of initiation, in positions alternating with the petals. **I.** Zygomorphic development of the androecium.

space in the locule in the most optimal way (Fig. 3F–H, J–K). In the young gynoecium we can see that the normal looking septa form massive separations between the locules (Fig. 3F–G). However, when looking at older stages, we can observe that the septa disintegrate in their outer parts: both walls of the locules become separated from each other (Figs. 3F, J–K, 4D–F). The fused inner margins of the carpels fall apart as the tissue between them disintegrates (Figs. 3J–K, 4E–F). In sections through the ovary, we can see that this disintegration is restricted to the peripheral parts of the septa, toward the ovary wall; more to the center, the massive structure of the septa is retained (Figs. 3I, 4C–D). It is striking that the massive parts of the septa are characterized by a high abundance of raphide bundles (Fig. 4D; arrowed). Figure 3I shows that some of the septa have already ruptured, breaking the connection between the central column and the ovary wall. When compared to the ovary wall, the septa appear to be rather thin and relatively delicate structures (Figs. 3I, 4E–F). We note that *I. niarnniemensis* is characterized by the presence of a sepal spur that is slightly bilobed at the tip (Fig. 3L).

Impatiens columbaria J.J. Bos—The purple flowers are arranged in groups of four to 10 in racemose inflorescences in the axils of the leaves. The flower primordia develop spirally

along the axis of the inflorescence in the axil of a bract (Fig. 5A). First, two lateral sepals arise (Fig. 5A–B). Next, the spurred sepal is initiated on the adaxial side of the flower, while on the abaxial side the floral apex enlarges significantly (Fig. 5C–D). On this side, two additional smaller sepals and the anterior petal now develop, in successive order (Fig. 5D–F). These three parts are almost from the beginning fused at the base (Fig. 5E–F). So, a pentamerous calyx, being less frequent within the genus, characterizes this species. The petal develops more rapidly than the sepals, and meanwhile, the four remaining petal primordia are initiated on the floral apex in two successive pairs (Fig. 5E–H). Five stamen primordia develop on an inner, alternating whorl. The development of the anterolateral stamens precedes the development of the posterolateral ones (Fig. 5G–H). During the further development of the androecium, its zygomorphic nature becomes more obvious (Fig. 5I). While the lateral petals form a triangular shape, they will become connate in pairs at the base (Fig. 5I). Now, five carpel primordia arise on the floral apex (Fig. 5J–L). They grow out and form the gynoecium, while the anthers are differentiating. Centrally, above the dorsal sporangia, the anther ends in a blunt tip (Fig. 6A), and on the abaxial side of the anther, the cells of the connective zone swell significantly (Fig. 6B). Especially the growth of the adaxial developing stamen,

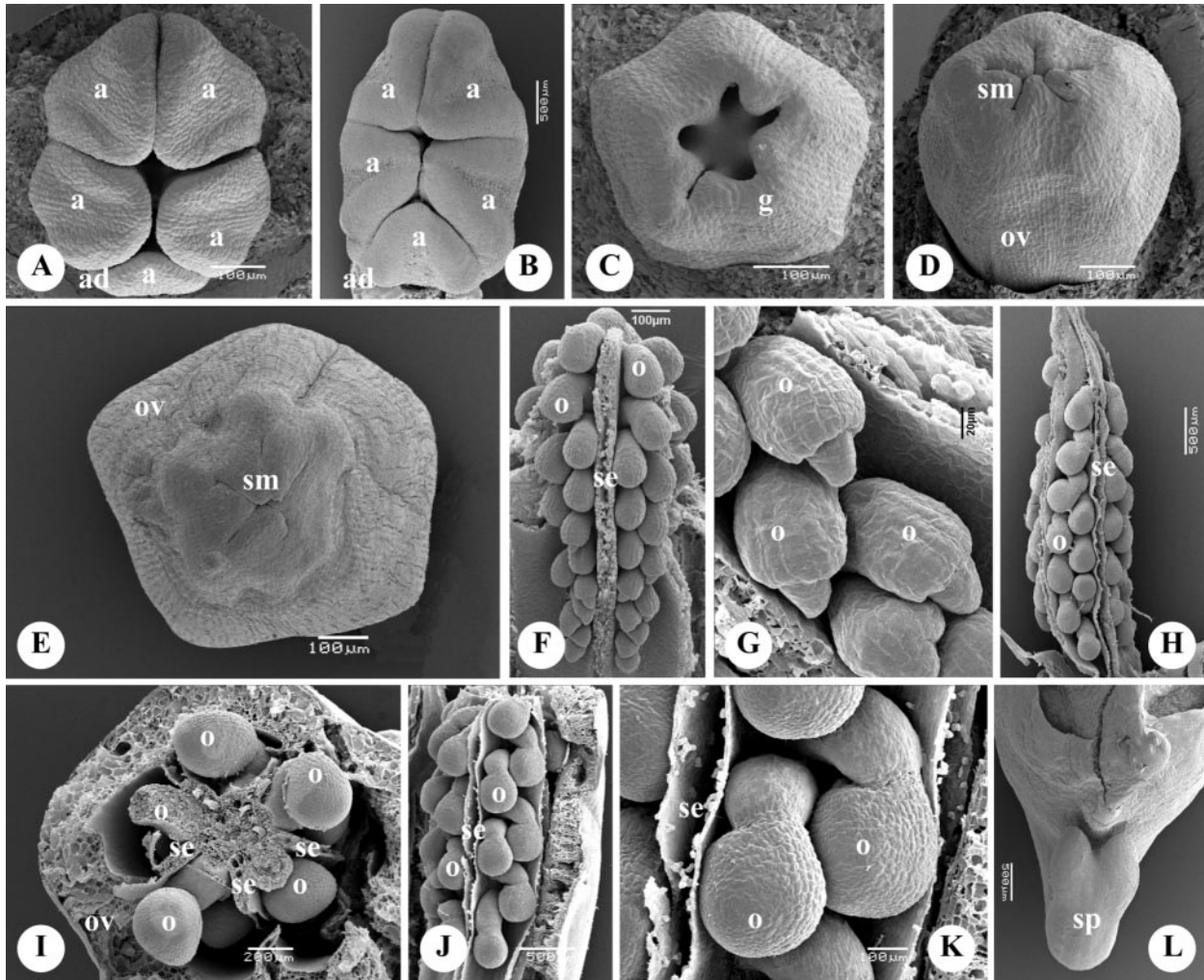


Fig. 3. Floral development of *Impatiens niarniamensis*. **A, B.** Differentiation of the dithecal, tetrasporangiate anthers. **C.** Development of the young gynoecium, in which five locules are being formed. **D.** Gynoecium with five developing stigma lobes. **E.** Top view of the developing gynoecium. **F.** In each locule, 10–15 ovules have been initiated in a basipetal sequence. **G.** Detail of the anatropous, unitegmic ovules. **H.** Lateral view of the ovules in the ovary; they possess long funiculi. **I.** Transverse section through the ovary: on the outside, the septa disintegrate and rupture from the ovary wall. **J.** Lateral view of the ovary showing the disintegration of the septa. **K.** Detail of a disintegrating septum. **L.** Detail of the developing spur of the posterior sepal.

which is the lowest one after resupination, will become gradually delayed (Fig. 6A). Individual filaments are hard to observe in this stage, but the anthers are inserted on a well-developed “stamen tube” (Fig. 6A; arrowed). In the next stage, however, filaments will develop, not as could be expected between the anthers and the “stamen tube,” but below the latter (Fig. 6C). The filaments form a kind of latticework around the gynoecium (Fig. 6C). They broaden toward their upper part where they fuse with each other and continue into the ring below the anthers (Fig. 6C). The anthers become connivent and open at the top through small slits in between the sporangia (Fig. 6C). In the meantime, the gynoecium has developed at the center, below the syngenesious stamens. The five carpels have merged into a barrel-like gynoecium (Fig. 6D). To the inside, the septa are getting shaped (Fig. 6D); they only fuse in the basal part of the ovary. The ring below the anthers consists on the inner side of five fused, scale-like appendages that partly grow out above the gynoecium (Fig. 6E–F). In the septate part of the ovary, the axile placentas are formed, and they fuse on the upper side, where the septa di-

verge (Fig. 6G). On the placentas, numerous ovule primordia develop (Fig. 6G). At the top, the gynoecium closes and about 10 lobes appear (Fig. 6H). A clear style cannot be recognized, although the gynoecium has a shallow constriction about one fourth of the way from the top (Fig. 6I). Meanwhile, the anatropous, unitegmic ovules develop in the superior ovary (Fig. 6J). From their initiation, they are arranged in several vertical series per locule (Fig. 6G, J–K). The disintegration of the septa was observed in this species as well (Fig. 6K). In the mature, spindle-shaped ovary, the ovules can be found almost exclusively in the central part of the locules (Fig. 6L). The ovary has a mainly synascidiate structure (Fig. 6L). When we look at the flower buds before anthesis, we notice a relatively long, resupinate pedicel, inserted in the axil of a bract (Fig. 6M). Due to the resupination, the spurred sepal becomes the lower one, and the flower gets its final position. The androecium and the gynoecium are completely enclosed by the posterior sepal and the anterior petal, which fit perfectly on each other; on the outside, the two lateral sepals can be observed (Fig. 6M). The rudimentary anterolateral sepals, which were visible in the

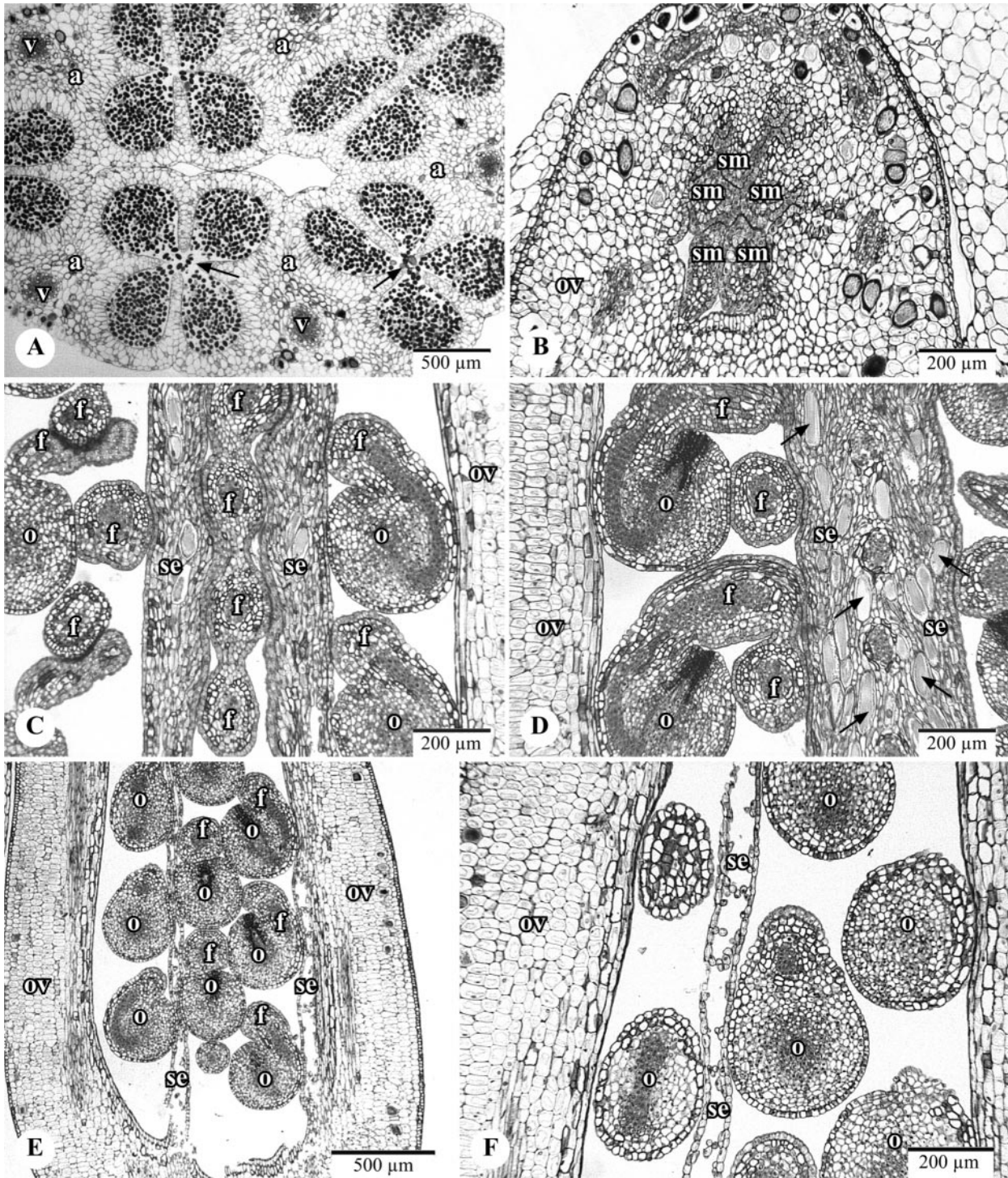


Fig. 4. Light micrographs of *Impatiens niarniamensis* stained with toluidine blue. **A.** Transverse section through the androecium showing connivent anthers; sporangia of adjacent anther lobes fuse (arrowed) before the pollen is released. **B.** Transverse section through the top of the gynoecium showing five stigmatic lobes. **C.** Longitudinal section through the ovary with ovules attached in one vertical row in between two septa. **D.** Longitudinal section through the central part of the ovary showing the anatropous ovules and massive septa, characterized by a high number of raphide bundles (arrowed). **E.** Longitudinal section through the peripheral part of the ovary with disintegrating septa; note the delicate structure of the thin septa when compared with the ovary wall. **F.** Detail of a disintegrating septum, in which only the outer margins remain.

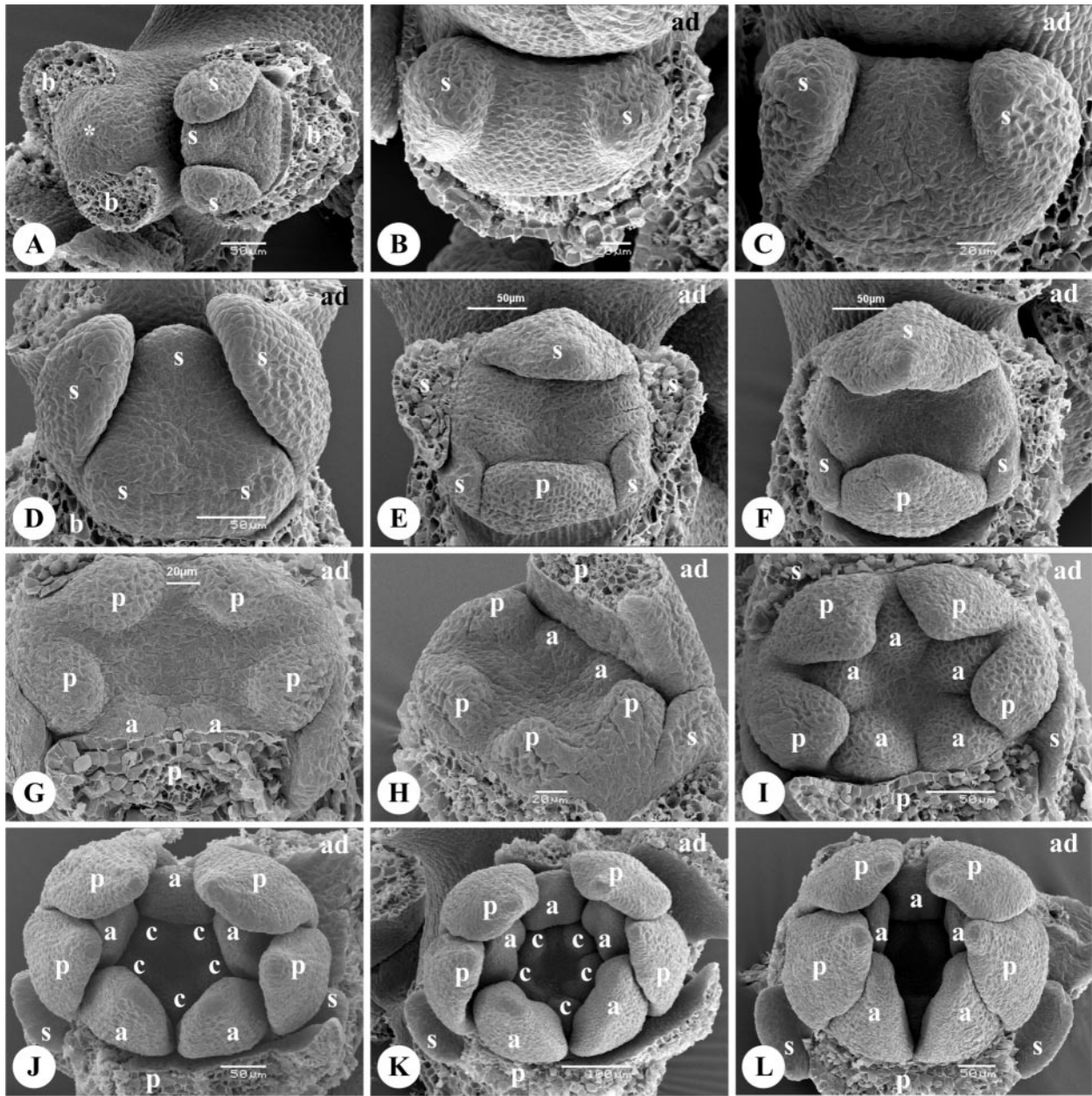


Fig. 5. Floral development of *Impatiens columbaria*. **A**. Top view of a developing flower at the top of the inflorescence axis. **B**. Stage in the development of the posterolateral sepals. **C**, **D**. The triangular floral apex has enlarged significantly at the abaxial side (bottom of the picture), while adaxially, the posterior sepal is initiated. **E**, **F**. Opposite the adaxial sepal (top of the picture), two anterolateral sepals and the anterior petal develop successively. **G**, **H**. Early developmental stage of the four lateral petals and initiated anterolateral stamen primordia. **I**. The lateral petals are now connate in pairs; the androecium has a zygomorphic appearance due to its unidirectional development, from the abaxial to the adaxial side. **J**, **K**. Alternating with the stamens, five carpel primordia have been initiated. **L**. The lateral petals and the stamens form a triangular shape while they grow outward.

earliest stages, have completely disappeared (Fig. 6M). It is worth mentioning that the spur develops rather late in the ontogeny (Fig. 6M). The spur forms an amphora-like shape and is slightly bilobed only at the extreme tip (Fig. 6N).

***Impatiens hawkeri* W. Bull**—The flowers in this species are solitary or in pairs in the axils of the leaves. Although the color is highly variable, the flowers in our material were white. The flower primordia are initiated in the axil of a bract (Fig. 7A). At first, two lateral sepals, which are often pointed in later stages, arise (Fig. 7A). When these sepals are removed,

we observe the initiation of the spurred sepal on the adaxial side of the floral apex (Fig. 7B). Unlike the other species studied here, all five petal primordia arise simultaneously (Fig. 7B). Nevertheless, the anterior petal develops more rapidly, resulting in a situation that is perfectly comparable with what we found in the two other species (Fig. 7C–D). There is no sign of any additional, rudimentary sepals (Fig. 7C–D). The four lateral petal primordia start to grow out as well, and alternating, a whorl of five stamen primordia develops on the inside (Fig. 7E). At the center on the floral apex, five carpel primordia arise simultaneously (Fig. 7F). They grow up and

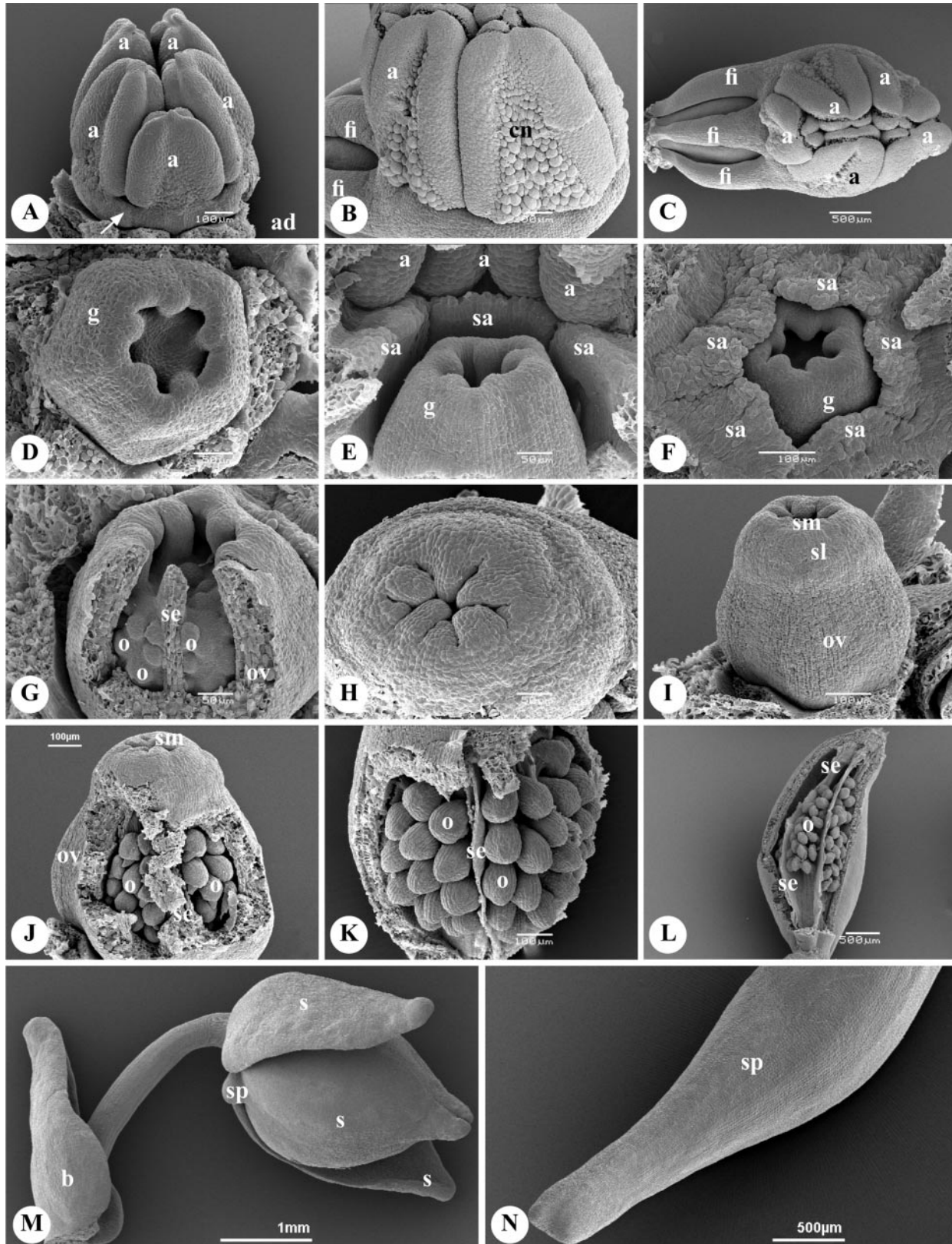


Fig. 6. Floral development of *Impatiens columbaria*. **A.** Adaxial view of the developing androecium; note that the anthers are inserted on a ring-like structure (arrow). **B.** Detail of the differentiating anthers, showing the swollen cells of the connective. **C.** Lateral view of the androecium with connivent anthers, enclosing the gynoecium. **D.** Top view of the young gynoecium with developing septa. **E.** Lateral view of the developing gynoecium surrounded by stamen appendages. **F.** Top view of the fused stamen appendages that partly cover the developing gynoecium. **G.** Lateral view of the opened ovary showing axillary placentae with ovule primordia. **H.** Top view of the gynoecium with developing stigmatic lobes. **I.** Lateral view of the gynoecium: a clear style cannot be observed, although

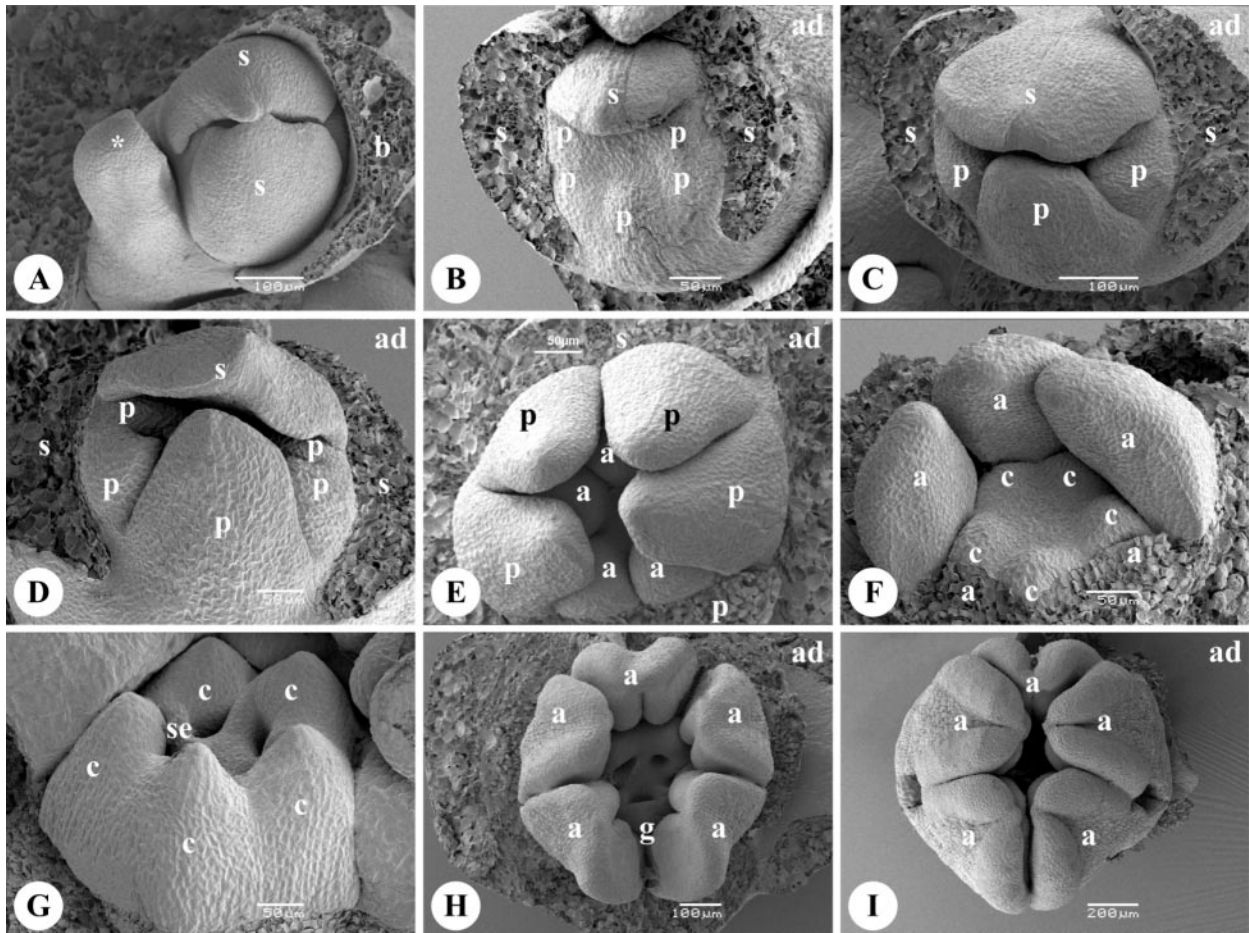


Fig. 7. Floral development of *Impatiens hawkeri*. **A.** Top view of a developing flower bud with two lateral sepals in the axil of a leaf. **B.** Development of the spurred sepal at the adaxial side of the flower (top of the picture); the five petal primordia have been initiated simultaneously. The anterior petal develops opposite the spurred sepal and the lateral petals arise in the zone between this sepal and the anterior petal. **C, D.** Developing flower bud showing the posterior sepal (top), the anterior petal (bottom), and the pairs of lateral petals (in between); the lateral sepals are removed. **C.** Top view. **D.** Lateral view. **E.** Basally connected lateral petals, alternating with five stamen primordia. **F.** Differentiating stamens; on the floral apex five carpel primordia arise. **G.** The carpels have grown upward to form the developing ovary; on the inside, five locules have been formed by inwardly growing septa that meet at the center. **H.** Top view of the differentiating anthers surrounding the developing gynoecium. **I.** Top view of the developing dithecal, tetrasporangiate anthers, which are inserted on broad filaments.

form caplike structures, while the central part of the apex is raised (Fig. 7G). The septa are congenitally fused with the column that grows up in the center (Fig. 7G). Consequently, five locules are being formed (Fig. 7G–H).

Now, the dithecal, tetrasporangiate anthers differentiate (Figs. 7I, 8A). Subsequently, the stamen appendages (arrowed in Fig. 8B) develop below the anthers (Fig. 8B–C), and they partly cover the gynoecium. The relatively short filaments greatly enlarge toward the top into fan-shaped structures (Fig. 8D). The stamen in front of the posterior sepal will, as in the other species studied, be limited in its development, resulting in a zygomorphic androecium (Fig. 8A–B). The lateral petals are hardly or just slightly connate in pairs (more clearly visible in younger stages, cf. Fig. 7D), but nevertheless strongly as-

sociated with each other (Fig. 8E). Hidden below the androecium, the barrel-like gynoecium closes at the top, where it has 10 lobes and five blunt projections (Fig. 8F–G). The latter are the carpel tips, still visible here as protuberances at the margin of the stigmatic surface (Fig. 8G). The septa are free in the upper part of the ovary (Fig. 8H), and they continue into five lobes in the stigmatic region (Fig. 8G). In front of the carpel tips, we find alternating with the septa lobes another five lobes, which are sometimes split up (Fig. 8G). In each of the five locules, about six anatropous, bitegmic ovules develop, arranged in one vertical series (Fig. 8I–L). As in both other species, we observed a disintegration of the septa during their development (compare Fig. 8I and 8L). They rupture from the ovary wall to enable the explosively dehiscent fruit to open.

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the gynoecium consists of a lower part (with ovules; cf. Fig. 6G) and an upper part, which might be interpreted as the stylar zone. **J.** Lateral view of the gynoecium with opened ovary with developing ovules. **K.** Ovules arranged in several vertical series per locule. **L.** Lateral view of an opened, spindle-shaped, mature ovary with ovules in the central part. **M.** Lateral view of a young flower bud in the axil of a bract; the sepal spur is still very small. **N.** Distal part of the developing sepal spur.

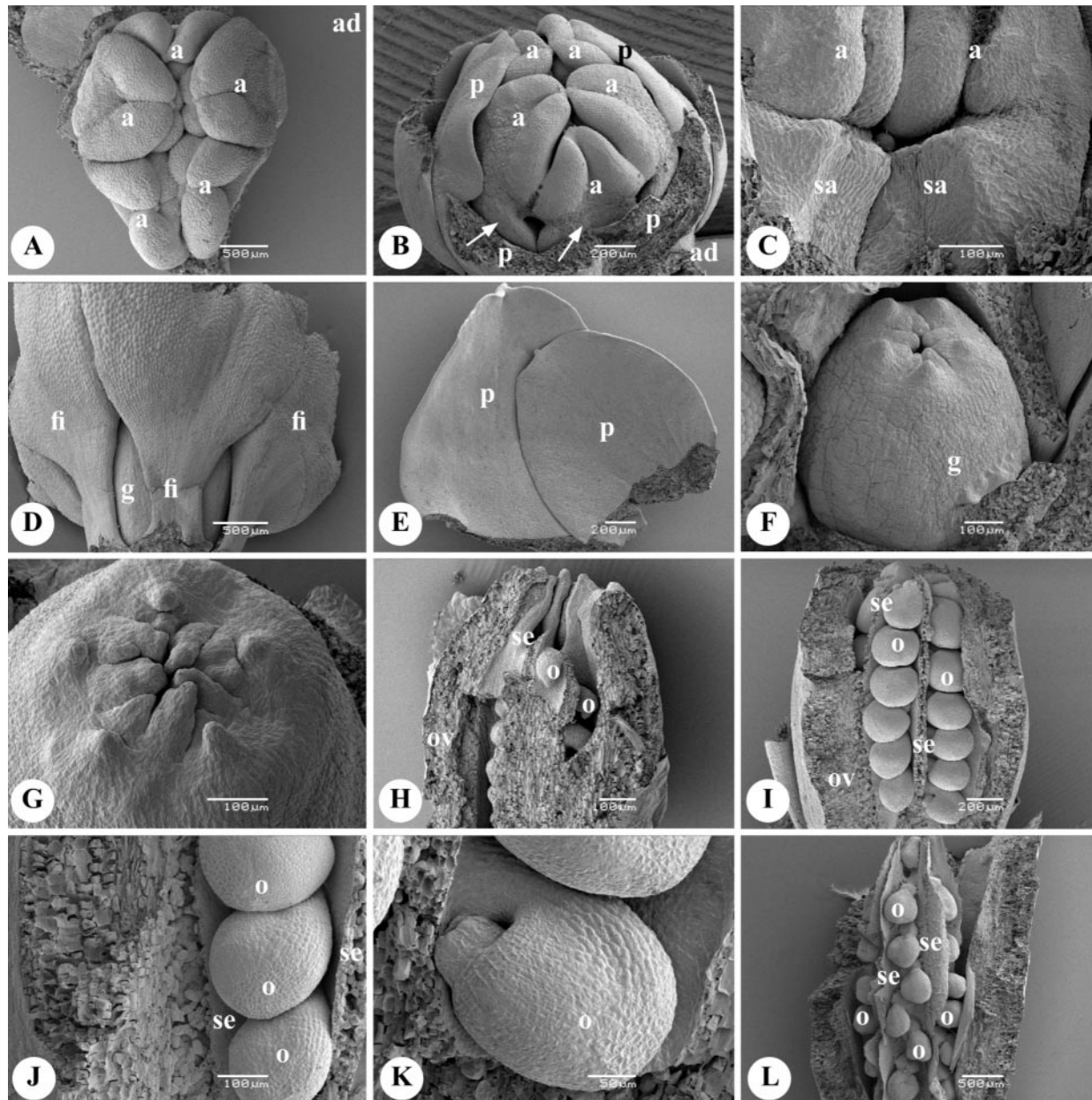


Fig. 8. Floral development of *Impatiens hawkeri*. **A.** Top view of the developing androecium; the anthers become connivent and enclose the gynoecium. **B.** Adaxial view of the androecium with developing stamen appendages below the anthers (arrowed); the posterior (adaxial) stamen is limited in its development when compared to the other stamens. **C.** Developing stamen appendages on the transitional region between anthers and filaments; they develop to the inside and will partly cover the gynoecium. **D.** Filaments have enlarged toward the top into fan-shaped structures surrounding the gynoecium. **E.** Pair of lateral petals. **F.** Lateral view of the developing gynoecium below the stamen appendages. **G.** Top view of the gynoecium showing about 10 stigmatic lobes and five blunt protuberances at the margin of the stigmatic surface. **H.** Lateral view of the opened gynoecium showing the incomplete fusion of the septa in the upper part (without ovules). **I.** Lateral view of the opened ovary with about six ovules per locule, in one vertical series. **J.** Detail of vertically arranged ovules, consuming all available space in a locule. **K.** Detail of an anatropous, bitegmic ovule. **L.** Lateral view of an opened ovary where the connection between septa and ovary wall has been broken; the septa are disintegrated when compared to septa in younger stages (cf. Fig. 8I).

DISCUSSION

In the past, Balsaminaceae were often placed in Geraniales (e.g., Cronquist, 1981) or in Sapindales (e.g., Scholz, 1964). Now, its position in the Ericales s.l. is well supported (Savolainen et al., 2000; Soltis et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; APG, 2003; Geuten et al., 2004). Although *Impatiens* is a popular pot plant and garden ornamental, few species are cultivated, and generally speaking, the ge-

nus is little studied. In particular, *I. balsamina* L., *I. glandulifera* Royle, *I. hawkeri*, and *I. walleriana* Hook. f. are widely grown (Wood, 1975; Grey-Wilson, 1983).

The floral structure, and in particular the perianth parts, vary, not only in color, but also in shape: characters such as the anterior petal, the lateral petals, and especially the spurred sepal are extremely variable, even within the same species (Hooker and Thomson, 1859). The rich variation in the floral structure may be linked to coadaptation with pollinators. Sev-

eral authors (e.g., Grey-Wilson, 1980a; Travers et al., 2003), for instance, find evidence of a relationship between nectar spur curvature and different sets of pollinators. On the other hand, Wilson (1995) suggests that selection for more successful visitation based on pollinator behavior might be much more important with respect to evolution of floral characters than adaptations to improve the mechanical fit between pollinator and flower.

Organization of the perianth—As long as the flowers of *Impatiens* have been studied, the precise relationships among the different floral parts have remained unclear (Grey-Wilson, 1980c). Relationships are blurred by the resupination of the flowers and the use of different descriptive terms regarding the position of the floral parts. In the past, several hypotheses have been postulated (for an overview of the old literature, see Payer, 1857). Generally, it is assumed that in most *Impatiens* species the number of sepals is reduced to three. However, from our data from *I. columbaria*, a species not particularly known as having a pentamerous calyx (Grimshaw, 1998), five sepals appear to be initiated early in the ontogeny. In later stages, the anterolateral sepals are no longer observable.

Röper (1830) was the first author who stated that the perianth of *Impatiens* consists of a calyx and a corolla that both are pentamerous. Payer (1857) studied the floral development of *I. glandulifera* and confirmed, like most of his colleagues, the findings of Röper (1830). According to Payer (1857), the two anterolateral sepals often stay rudimentary or disappear in later stages. Although we have no doubts about the conclusions of Payer (1857), we would like to stress that the rudimentary sepals are not initiated in all *Impatiens* species, as is clearly shown by our results from *I. niarniamensis* and *I. hawkeri*. Here, we can only observe an enlargement of the floral apex on the abaxial side, but anterolateral sepals are not initiated.

Warburg and Reiche (1895) postulate that the initiation of the calyx follows a 2/5-spiral. According to these authors, only three sepals characterize most *Impatiens* species; the development of the third and the fifth are suppressed. If present, they are visible as small structures that have shifted towards the median axis (Warburg and Reiche, 1895). As opposed to what one would expect, the anterolateral sepals (sepals three and five) are initiated last, after the appearance of the posterior sepal (sepal four). Warburg and Reiche (1895) remark that in species with five sepals, the fourth one develops before the third one, indeed, which—according to them—may be the result of the rudimentary nature of the third and the fifth sepal. Our results support their descriptions.

Grey-Wilson (1980c) studied the floral anatomy of *Impatiens* and found that some species contain rudiments of the vascular traces of the often-missing sepal pair. From their position, he concludes that the anterolateral pair has been reduced. This is supported by the fact that in species with five sepals, the anterolateral pair is always smaller and thinner than the posterolateral one; moreover, it is positioned more to the inside (Grey-Wilson, 1980c). Our ontogenetic results from *I. columbaria* confirm the conclusions of Grey-Wilson (1980c): the rudimentary sepals develop in anterolateral position, and they are inserted somewhat higher up on the floral apex (more to the inside) when compared to the posterolateral sepals. They are also closely connected with the adjacent anterior petal. On top of that, the moment of initiation of the anterior petal differs from what one would expect: the anterior petal develops si-

multaneously with or immediately after the initiation of the posterior sepal, and commonly, well before the lateral petals appear.

The “disappearance” of the rudimentary sepals during ontogeny in some species can be explained through postgenital fusion with the adjacent anterior petal (which is often positioned on the same whorl) or through resorption by the further developing receptacular tissue. In species lacking the anterolateral sepal primordia, we could speak of a similar kind of fusion, but then it would be congenital. We believe that in the course of evolution the anterolateral sepals do not actually disappear, but gradually fuse with the anterior petal. As a result, in some species this is not a petal in the strict sense, because it is composed of parts from the calyx and the corolla that have become united. The often partly sepaloid appearance of this organ (which for convenience we will further describe as the anterior petal) supports this hypothesis (already formulated by Ramadevi and Narayana, 1989), as does the fact that the anterolateral petals, when present, are positioned more to the inside of the flower.

Wood (1975) mentions (but rejects) an old interpretation of the perianth, which was thought to have four sepals and four petals. The fourth sepal (in fact the anterior petal) was reported to have a petaloid appearance and had an incision in the center. According to this interpretation, the incision suggests that this organ is in fact composed of two fused sepals. The latter is interesting with respect to our hypothesis in which the anterior petal is composed of several perianth parts as well. Floral anatomy also supports our hypothesis because the vascular traces for the anterolateral sepal pair are found at both sides (and only slightly to the outside) of the trace for the anterior petal (Grey-Wilson, 1980c). Ramadevi and Narayana (1989) studied the floral anatomy of *Impatiens* and found that from the ring-like vascular tissue in the pedicel first the traces to the posterolateral sepals diverge. Next, again two traces diverge, one leading to the posterior sepal, the other one splitting up into three bundles for the anterior petal and the anterolateral sepals, all three of them entering the composed perianth part formed by the union of the anterior petal and the anterolateral sepals (Ramadevi and Narayana, 1989). In *I. elegans* Bedd., they observed that the vascular traces of the lateral petals, and the common trace for the composed perianth part are arranged on the same whorl (Ramadevi and Narayana, 1989).

Undoubtedly, the ontogeny of many species is insufficiently known. Hence, we expect that many other species will show rudiments of the anterolateral petals in their early ontogenetic stages. Furthermore, in *I. hawkeri* we occasionally observed rudimentary anterolateral sepals, even in mature flowers, whereas most flowers do not have any signs of these sepals. Likewise, Hooker and Thomson (1859) already mentioned that anterolateral sepals may be absent or present within the same species. Some species appear to be very plastic regarding the development of anterolateral sepals, or in other words, regarding the degree of congenital fusion of these sepals with the anterior petal.

Fusion of the lateral petals—The different fruit type and the presence of five free petals morphologically separate *Hydrocera* from *Impatiens*. Within the family, free petals are considered to be plesiomorphic. *Impatiens* is generally characterized by the presence of lateral petals connate in pairs. Nevertheless, the degree of fusion often varies among species (and maybe within species as well). In the past, it was unclear if

these were two bilobed petals rather than four petals connate in pairs (Grey-Wilson, 1980c). According to Warburg and Reiche (1895), most species possess three petals, and they explain this feature by assuming that from the theoretically five petals, the four lateral ones are fused. They find evidence for this hypothesis in the presence of a central incision in the upper margin of the bilobed structures. However, Grey-Wilson (1980c) proved on the basis of floral anatomy that each of the petals has its own independent vascular trace and that all petals develop separately. Our floral ontogenetic results support this conclusion: the lateral petals are formed from four separate petal primordia. We think that the fusion between the lateral petals on either side of the flower is insufficiently studied to use it as a morphological character to separate *Hydrocera* from *Impatiens*. It cannot be excluded that future studies will reveal *Impatiens* species with five free petals as well, when the enormous diversity in shape, size, and fusion of the lateral petals is taken into account. On top of that, petals of *Impatiens* always develop from separate primordia and as far as known, they are never fused congenitally. A lot depends, of course, on where the borderline between "free" and "fused" is drawn. According to Wood (1975), for example, the lateral petals of *I. walleriana* are mainly free and only slightly fused at the very base. The situation in this species might as well be stated as free (Warburg and Reiche, 1895).

Androecium—The zygomorphy present in the corolla is found in the androecium as well; as we described, the anterior stamens grow larger than the posterior ones. The scale-like appendages on the inner and upper side of the filaments form a kind of cap that partly covers the gynoecium. The five stigmas are coherent and in many species, they only spread after the androecium has been dropped.

The anthers lie closely together and adjacent anther lobes fuse (Raghuvver and Narayana, 1994). The four sporangia that are involved, merge to form a common space, which contains the pollen of both thecae (cf. Fig. 4A; arrow). The pollen is released through a slit at the top of this common space via the pressure created by the swollen cells in the connective region of the anther (Loew, 1892; Warburg and Reiche, 1895). The pollen is presented on the depression enclosed by the edges of the connivent anthers, the so-called Pollenstreufäche (Loew, 1892). Due to the resupination of the flower, the Pollenstreufäche is positioned below the stigmatic region. As a result, self-pollination is avoided (Loew, 1892). When the pollinators search for nectar in the sepal spur, they are loaded with pollen from the Pollenstreufäche. According to Loew (1892), in some species in which the stigmas do not open, pollen from another flower on the head of the pollinators is positioned in the pollination chamber (cf. Loew, 1892), which is reached by a slit between the anterior stamens. The stamen appendages form a small crown or funnel, with five lobes catching the pollen. The so-called pseudostigmas (Loew, 1892) bring the pollen into the neighborhood of the stigmas. In many other species, the androecium is shed, and the coherent stigmas spread and expose their receptive surface, as we mentioned before. According to Warburg and Reiche (1895), the stamen appendages might as well have a function in avoiding self-pollination.

Gynoecium—Traditionally, the gynoecium is always considered to be five-carpellate, as is the case in the species studied here. However, Shimizu and Takao (1982) have shown that

some species of *Impatiens* possess tetramerous gynoecia with four-locular ovaries.

In general, the style is reported to be very short or missing: a clear distinction between style and ovary cannot be observed. Nevertheless, the septa are not fused in the upper part of the ovary, i.e., the hemisymphiccate zone sensu Leinfellner (1950). This zone has no ovules and might as well be considered to be a styler zone. The situation could easily be compared with that of a lot of other Ericales, in which the septa continue in the internal lobes of the style, leaving a central, styler canal with as many branches as locules. Shimizu and Takao (1982) mention a styler canal for all species they have investigated. Ramadevi and Narayana (1989) describe the ovary as five-locular in the ovule-bearing part and unilocular at the top because of the presence of incomplete septa there. It can be argued that the lobes on the top of the gynoecium do not represent five individual stigmas, but rather one composed stigma, consisting of several lobes. Similar cases can be found in, for example, Ericaceae, where the styler lobes protrude at the surface of the stigma.

Boesewinkel and Bouman (1991) investigated ovule development in *Impatiens*. They conclude that ovules are bitegmic, unitegmic, or intermediate. The changeover from bitegmic (plesiomorphic) to unitegmic (apomorphic) is caused by the fusion of the dermal integument initials together with a shift and a growth restriction of the outer integument primordium (Boesewinkel and Bouman, 1991). Due to the fusion, a common zone develops in intermediate species, which is only divided in two individual integuments at the top (Boesewinkel and Bouman, 1991). Nonetheless, completely unitegmic species also occur, for instance, *I. niammiamensis* studied here. Unitegmic ovules are particularly typical of sympetalous groups (Boesewinkel and Bouman, 1991). The combination of bitegmic and tenuinucellate ovules, as is commonly found within *Impatiens*, is less widespread. It is interesting that this situation is also typical within another group of Ericales s.l., namely, the primuloid clade.

Ovule arrangement—Shimizu and Takao (1982) distinguish between uniseriate and biseriata arrangement of the ovules within a locule. Species with both types occur as well. Moreover, these species often possess intermediate types of arrangement, making the exact insertion of the ovules difficult to judge (Shimizu and Takao, 1985). According to the same authors, a reductive trend can be followed in the number and the position of the ovules: from several to one ovule or none and from biseriata to uniseriate (Shimizu and Takao, 1982). Because of the alternation in the arrangement of the ovules, uniseriate species may seem to have biserially arranged ovules in transverse sections, and on the other hand, transverse sections of biseriata species might have only one row of ovules.

Shimizu et al. (1996) studied six species from the subgenus *Acaulimpatiens* Warb. and found that the ovules in a locule are arranged in four to eight vertical rows. According to Shimizu et al. (1996), this character does not occur outside this subgenus, with the exception of *I. siamensis* T. Shimizu, in which the ovules are arranged in three to four rows. Nevertheless, it is evident from our results that in *I. columbaria*, ovules are arranged in several series as well. Up to the present, nothing is known about the fruit of *I. columbaria* (Grimshaw, 1998). Most probably, future studies will reveal that also other species of *Impatiens* show this feature.

Fruit dehiscence—The particular dehiscence mechanism of the fruits is made possible by the disintegration of the internal tissue of the septa. It is unknown whether the raphide bundles, which are, in fact, needle-shaped crystals of calcium oxalate, play a role in the disintegration of the septal tissue. Possibly, oxalic acid is formed, which might be able to destroy the cellulose walls in the outer parts of the septa. A similar process occurs in the disjunctive tissue of the anthers of some Ericaceae (Matthews and Knox, 1926). As a result of the particular development of the septa, the presence of a completely septate ovary with axile placentation is not an obstacle to explaining the explosive dehiscence of the fruit. Wood (1975) describes the septa of *Impatiens* as delicate structures that are compressed by the developing ovules. The explosive dehiscence of the fruit is the result of the combination of an outer, highly turgescer epidermis tissue and swollen parenchyma cells beneath the epidermis, and the nonturgescer tissue further in (Warburg and Reiche, 1895). Raghuvver et al. (1993) studied the anatomy and dispersal of what they called the dehiscent fruit of *Hydrocera triflora* (L.) Wight & Arn. They maintained that the five-seeded fruit is a capsular berry that opens septically: the wall of the imbibed fruit (the fruits float on and are dispersed by water) normally splits from the base upwards along the radii of the septa (Raghuvver et al., 1993).

Special adaptations of the flower related to protandry, the particular floral structure with its zygomorphy and deviations in the perianth organization, along with the exceptional opening mechanism of the fruit linked to the special morphology of the ovary, make the flower of *Impatiens* a highly modified structure. Moreover, floral diversity in the genus is extremely high. In the present study, we investigated three species of *Impatiens* in order to comment on general trends in flower morphology and evolution. Nevertheless, detailed morphological and anatomical studies of a broader range of species are needed to contribute to a better understanding of floral evolution and fruit morphology in this species-rich genus.

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