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Notes on the floral anatomy of *Annona haematantha* Miq.: an unexpected and specialized annonaceous corolla

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ABSTRACT

The South-American species *Annona haematantha* Miq. exhibits a very puzzling corolla, which was previously interpreted as two stacked corolla tubes. An anatomical study was undertaken in order to solve this question. The outer and inner petals are fused at their base in a wide tube not appressed to the reproductive organs. The inner petals are adaxially modified into prominent glands on the proximal ¾ of their length. The receptacular vasculature, as well as androecial and gynoecial structures are otherwise wholly in accordance with the floral anatomy of other known *Annona* L. species. Such a localized adaptation suggests a peculiar pollination process and widens the range of nutritious tissue patterns recorded in Annonaceae flowers. The pollination system probably involves night-flowering, thermo-genesis, scent emission, and intervention of scarab beetles.

KEY WORDS
Annonaceae,
floral anatomy,
pollination,
scarab beetles.

RÉSUMÉ

*Notes sur l'anatomie florale d'*Annona haematantha *Miq. : une corolle annonacéenne inattendue et spécialisée.* L'espèce sud-américaine *Annona haematantha* Miq. présente une corolle très curieuse, qui était auparavant interprétée comme deux corolles concentriques. Une étude anatomique a été entreprise afin de résoudre cette question. Les pétales externes et internes sont fusionnés à leur base en un large tube non apprimé sur les organes reproducteurs. Les pétales internes sont modifiés adaxialement en glandes proéminentes sur les ¾ de leur longueur. La vascularisation réceptaculaire, ainsi que les structures androéciale et gynoéciale sont par ailleurs tout à fait conformes à l'architecture florale des autres espèces connues d'*Annona* L. Une telle adaptation localisée suggère un processus de pollinisation particulier et élargit la gamme des tissus nutritifs observés dans les fleurs d'Annonaceae. Le système de pollinisation implique probablement une anthèse nocturne, la thermogénèse, l'émission d'odeurs et la cantharophilie.

MOTS CLÉS
Annonaceae,
anatomie florale,
pollinisation,
scarabées.

INTRODUCTION

Annonaceae (Magnoliales) is a diverse family of trees and lianas with about 109 genera and around 2500 species and with a pantropical distribution (Maas *et al.* 2023: 11). The family is an important ecological component of lowland and mid elevation rain forests worldwide. In addition, Annonaceae presents a wide array of flower morphologies (van Heusden 1992), albeit based on a similar floral architecture of three sepals, three free outer petals and three free inner petals.

Annona L. is one of the most species rich genera of the family with around 170 accepted species (Rainer 2001), mainly centered in the Neotropics and with three or four species in Africa (Couvreur *et al.* 2022). In addition, the genus exhibits one of the most diverse display of flower variation in the family in terms of petal number (ranging from six to three), petal shape (e.g., presence of the unique winged petals) and petal fusion (free versus fused). In most cases this variation was used to circumscribe different genera in the past (e.g., *Rollinia* A.St-Hil., *Raimondia* Saff.). Molecular phylogenetic analyses (Guo *et al.* 2017; Larranaga *et al.* 2019) supported however the inclusion of all this variation in the same genus *Annona* (Rainer 2007).

The South-American species *Annona haematantha* Miq. was described by Miquel (1849). It is recorded as a liana, at least in its adult form (Maas *et al.* 2007), mainly growing in the understory of non-inundated forests, especially in Guyana, Suriname, French Guiana and northern Brazil, as well as Peru, Ecuador and Amazonian Colombia (Maas *et al.* 2023: 81). Miquel described the species from a single collection made in 1842, *Hostmann & Kappler 1191*. The collectors indicated that the plant was from Suriname and noted it was scandent, with blood-red flowers, and occurred in marshes. Many decades later in 2007, when working on the Ducke Reserve Flora in the Amazonian Brazil, Maas *et al.* (2007) completed the description based on another specimen *Asunçao P.A.C.L. 132,* collected in the Ducke Reserve in Northern Brazil, near the city of Manaus.

Maas *et al.* (2007) described the flower of *Annona haematantha* as having two distinct tubes "Outer petals connate, tube 5-8 mm long" and "Inner petals connate, tube ca. 7 mm long". This suggests that both inner and outer whorls are independently fused. It is not uncommon for Annonaceae species to show petals fused into a corolla tube but when present they are formed from the fusion of both the inner and outer whorls together (e.g., *Disepalum* Hook.f., *Hexalobus* A.DC, *Isolona* Engl.), rather than independently. Thus, if verified *Annona haematantha* would represent a unique floral morphology for Annonaceae. More recently however, the description of *Annona haematantha* was revised (Maas *et al.* 2023: 81) with the authors indicating "outer petals connate into a tube 5-8 mm long "and "inner petals valvate, red, adnate to outer ones". Here, the inner petals are fused to the outer ones but not between them. They also indicated that another species, *Annona ambotay* Aubl., presents a similar morphology with the smaller inner petals adnate to the outer ones, suggesting a close relationship between them, but can be distinguished by their habit (Maas *et al.* 2023). Indeed, *A. haematantha* is a liana while *A. ambotay* is a tree up to 10 m tall (Maas *et al.* 2023). There appears thus to be some confusion around the floral structure of *A. haematantha*, with two main hypotheses: outer and inner petals independently fused or inner petals adnate to the outer ones.

The objective of this study is to anatomically describe the flower of *Annona haematantha*, specifically to test which hypothesis is supported. We then used our observations to discuss different aspects about flower anatomy at the genus and family levels, and propose consistent hypotheses about the pollination syndrome of this interesting species.

MATERIAL AND METHODS

A floral bud of *Annona haematantha* Miq. (Fig. 1) was removed from a herbarium specimen of the P herbarium (French Guyana, Saül, 4.VI.1986, *Mori S.A. & Gracie C.A. 18315* [P02027641]). It was restored using NH_4OH 10% aq., at 60°C during 48 h and postfixed by FAA (90% ethanol 70%, 5% formalin, 5% acetic acid) for 48 h, then soaked in a preservative mixture of water, ethanol and glycerol (equal volumes). The bud was then dehydrated through a t-butyl series and embedded in paraffin (melting point: 58-60 °C; Gerlach 1984). Serial transverse sections (30 slides) were cut at a thickness of 15 µm by a rotary microtome Leitz 1512 (Germany). Almost all the sections (in 28 slides) were left unstained as conducting tissues are well distinguishable, and to avoid any loss of this scarce material. Two of them (slides 26 and 30) were stained using Astrablue [Chroma® 1B 163] 0.5% aq. and Ziehl's fuchsine [RAL® 320490-1000] 10% aq. in order to bring to the fore the secretory tissues in the corolla. All slides were mounted in Eukitt [O. Kindler GmbH® E0214], and are kept in the plant histological collection of the Muséum national d'Histoire naturelle of Paris, under the range reference *Deroin 241*.

Floral vasculature was reconstructed by making drawings of the serial sections using a camera lucida, and then by superimposing tracing papers on them.

Microphotographs were taken with a Zeiss microscope (Imager M2) combined with a camera AxioCam 305 color.

RESULTS

Receptacle vasculature (Figs 2; 3A-F; 5)

In the cross-section of the pedicel just below the level of the calyx insertion, there is a stele of *c.* 15 bundles around a pith comprising some complete sclerous diaphragms (Fig. 2A). From these bundles, three strands emerge at the receptacle base (Fig. 2B-D) and correspond to fused lateral sepal bundles (synlaterals, sls). At the base of the receptacle, three alternate strands arise (Fig. 2 E-H), merging the median sepal bundles, median inner petal bundles and even higher a quarter of stamen traces. These are thus the trunks of a cortical vascular system (CVS) belonging to the sepal-petal-staminal pattern (ms + mpi + e). A third crown diverges above (Fig. 2H, I), consisting of three bundles fusing the median outer petal bundles and another quarter of stamen traces. The CVS is completed by six intermediate bundles merging the petal synlaterals and half of the stamen traces (Fig. 3A, B). After supplying the corolla, the CVS ends in a crown of *c.* 24 trunks (Fig. 3C-F), which are the sources of the whole androecial vasculature, feeding *c.* 280 stamens. No additional contribution from the stele was observed.

Anther histology (Fig. 4)

At its base (Fig. 4A) the anther is slightly extrorse, with wide pollen sacs. Two patterns of parenchyma occur in the connective: a light abundant parenchyma, with medium-sized cells and another parenchyma located in small divided patches beneath the epidermis and made of smaller cells with a reddish (fuchsinophilous) content. Some scattered large secretory cells occur too. Halfway up (Fig. 4B) the anthers appear more extrorse with somewhat wider pollen sacs, a more abundant reddish parenchyma, centered around the collateral vascular bundle and anchor-like in cross section. Two large secretory cells are found on either side of this central tissue.

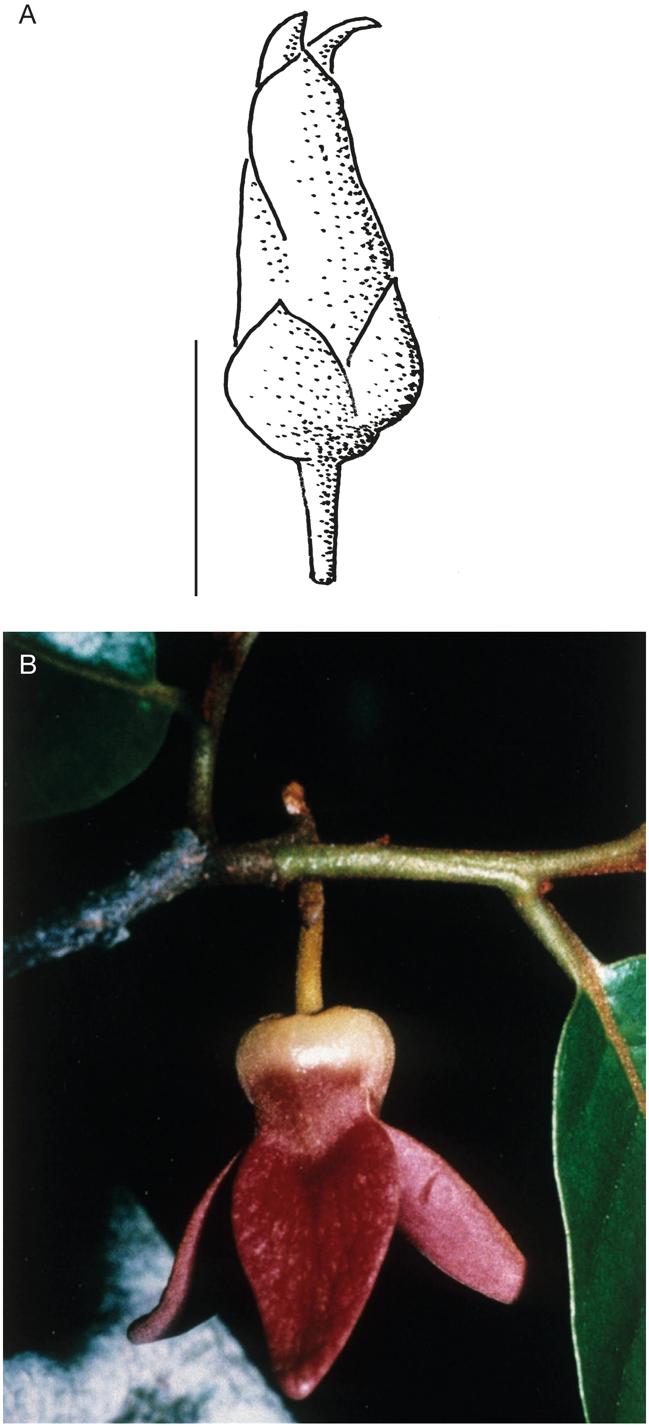

Fig. 1. — **A**, Morphology of the studied floral bud (*Mori S.A. & Gracie C.A. 18315* [P02027641]); drawing: Thierry Deroin; **B**, field photo of the anthetic flower of *Annona haematantha* Miq., (photo Marie-Françoise Prévost, EZID number http://n2t.net/ark:/65665/m3f963709f-d8a1-45a8-b30b-23a9eb0d6ad5). Scale bar: A, 1 cm.

Gynoecium (Fig. 3G-P)

The apical stele (*c.* 12 bundles) breaks up and feeds the gynoecium (Fig. 3G-K). Fourteen carpels are inserted at the flat top of the receptacle, loosely arranged in two whorls (10 and four carpels). Each carpel exhibits three traces (one median and two lateral bundles). The vascular supply of the

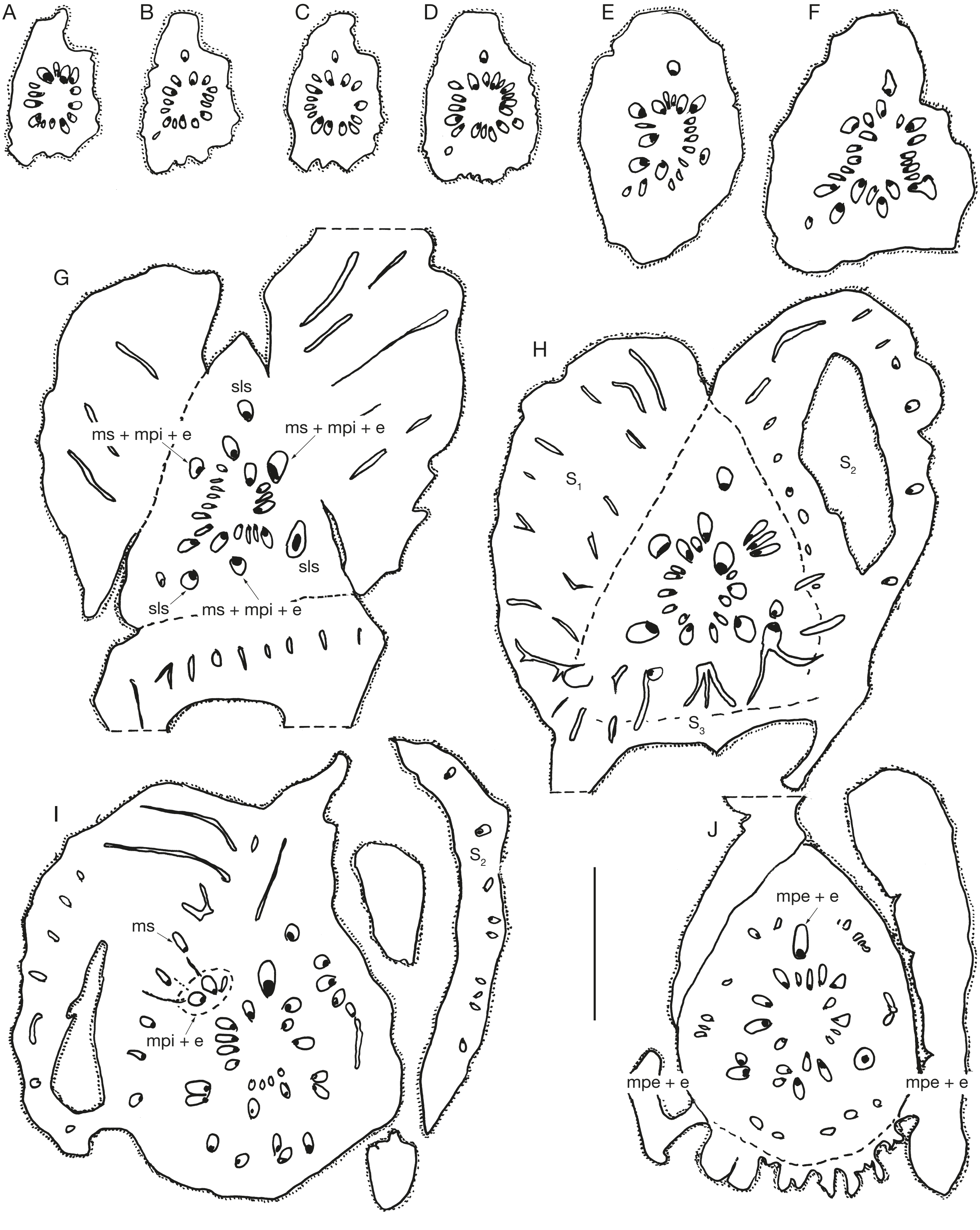

Fig. 2. — Transverse ascending sections of the flower of *Annona haematantha* Miq., pedicel and receptacle (**A**-**F**), calyx (**G**-**I**) and corolla (**J**) insertion levels. Abbreviations: **e**, stamen bundle; **mpe/mpi**, median bundle of external/inner petal; **S**, sepal; **sls**, synlateral sepal bundle. Drawings: Thierry Deroin. Scale bar: 1 mm.

sole ovule was not visible. As usual in the genus, carpels are fused by their sides (pseudosyncarpy, Fig. 3K-M), and the solid stigmatic plate (Fig. 3N-P) belongs to the "modèle compact" pattern (Deroin 1991), i.e., the "Type 1" described by Briechle-Mäck (1994: 99).

Glandular inner petals (Figs 6; 7)

The corolla is gamopetalous, tubular at the base (Fig. 6A, B), and not appressed to the sexual organs, which are inserted on a somewhat convex receptacle. Outer and inner petals are more or less equal (inner petal length is not half that of

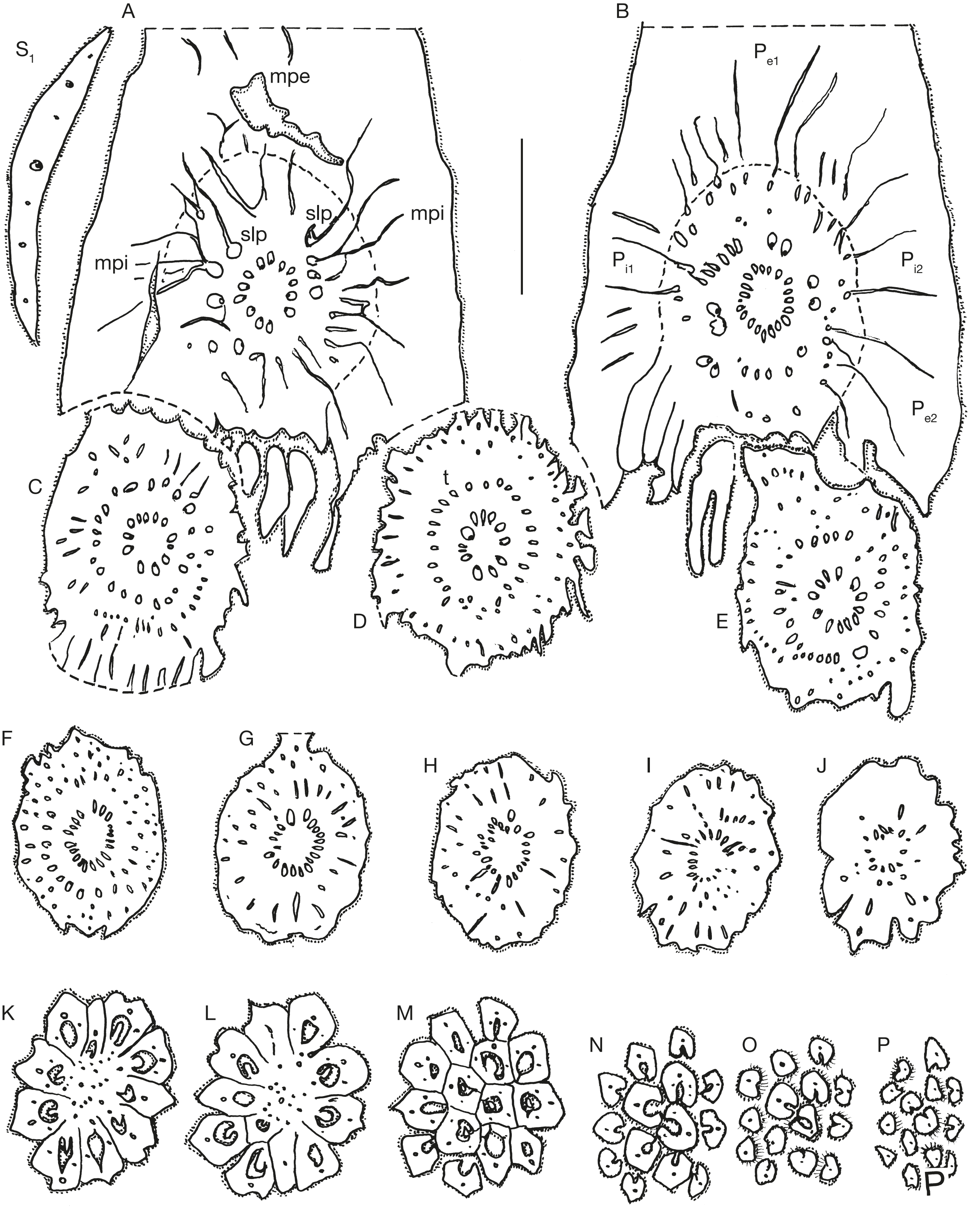

Fig. 3. — Transverse ascending sections of the flower of *Annona haematantha* Miq., corolla insertion (**A**, **B**), androecial vasculature (**C**-**F**), basal gynoecial vasculature (**G**-**J**), gynoecium (**K**-**P**). Abbreviations: same as in Fig. 2; **Pe**, external petal; **Pi**, inner petal; **slp**, synlateral petal bundle; **t**, staminal trunk. Drawings: Thierry Deroin. Scale bar: 1 mm.

outer ones, as quoted by Fries 1959: 149) and show similar scattered vasculatures (*c.* five bundles each, basally 3-trace), while their apices are alike too (Fig. 7E).

The inner petals have modified glands in their free parts (Figs 6C, D; 7A, B) at about the proximal two thirds of the corolla height (in the bud). In cross section (Fig. 7C, D)

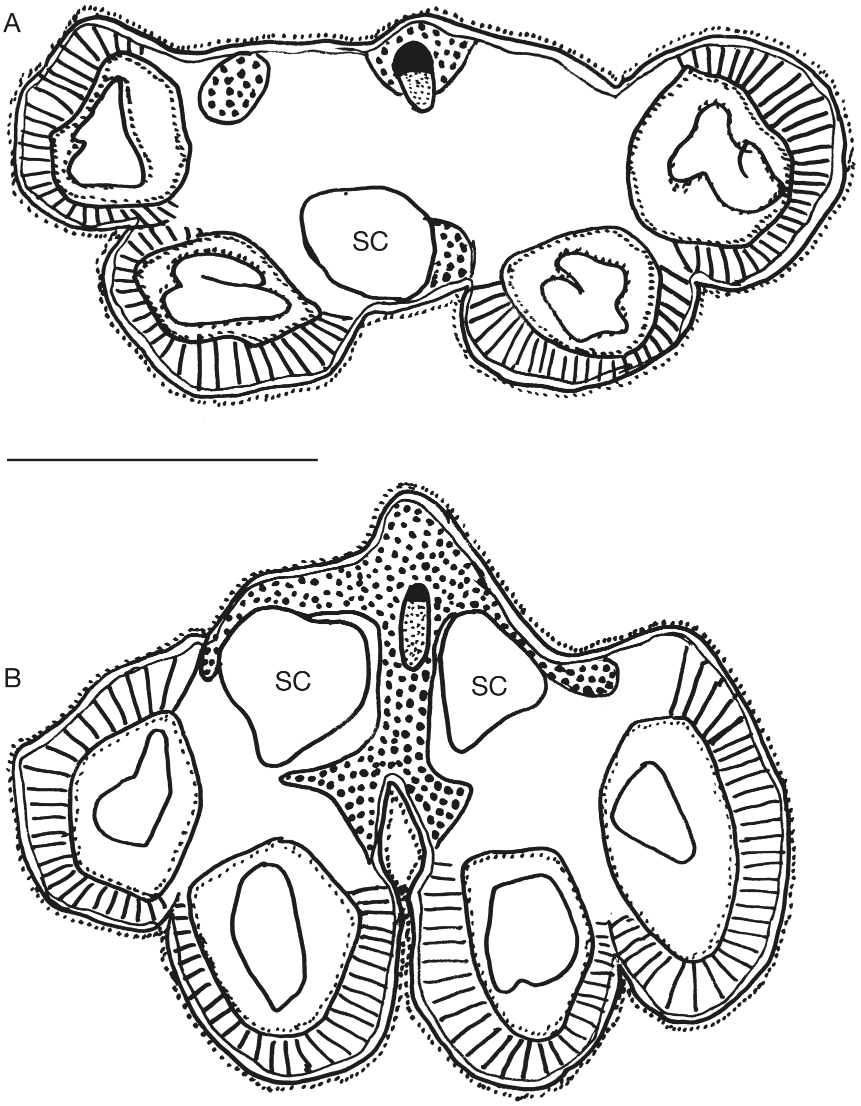

Fig. 4. — Anther anatomy of *Annona haematantha* Miq., at basal (**A**) and middle (**B**) levels. Abbreviation: **sc**, secretory cell. Xylem black, phloem stippled, reddish parenchyma **dotted**. Drawings: Thierry Deroin. Scale bar: 100 µm.

they exhibit at this level a peculiar histology. From inside to outside:

1) a thin epidermis of somewhat papillate cells with dense nuclei and blue – possibly mucilaginous – cytoplasm. This layer covers a deeply corrugated surface;

2) two to six layers of a light parenchyma, with small thin-walled cells, showing large nuclei with nucleoli. Then *c.* six layers of wider parenchymatous cells with large pinkish nuclei and starch grains (Fig. 7D), comprising numerous secretory cells;

3) phloem-xylem bundles outlined by reddish cells, rather similar to those recognized above in the “anchor” tissue of anther;

4) a parenchyma of *c.* eight layers of angular cells, tangentially flattened, somewhat lignified in places, followed by five or six layers of smaller round cells, including some scarce but well-lignified sclereids;

and 5) an hypodermal layer below an outer epidermis with minute cutinized cells and curled simple hairs.

DISCUSSION

The anatomical study of *Annona haematantha* shows that the descriptions of Maas *et al.* (2007; 2023) are incorrect, and that the outer and inner petal whorls are not independently fused nor are the inner petals simply “adnate” to the outer ones. Rather, we show that the corolla is fused into a single whorl (Figs 6A; 7) and the lateral petal bundles are fused characteristic of true sympetaly (Fig. 5). However, even though the whorls are fused, the inner petals remain differentiated morphologically in relation to the outer ones. The overall architecture of the floral vasculature conforms with what is described in some other *Annona* species, such as *A. muricata* L., *A. senegalensis* Persoon or *A. squamosa* L. (Deroin 1988a), but is distinct from these by the extent of fusion. Here, all lateral traces are fused together in the perianth whorls, as in the CVS of the sepal-petal-staminal pattern, with a low number in staminal trunks (24, instead of 30-45 recognized

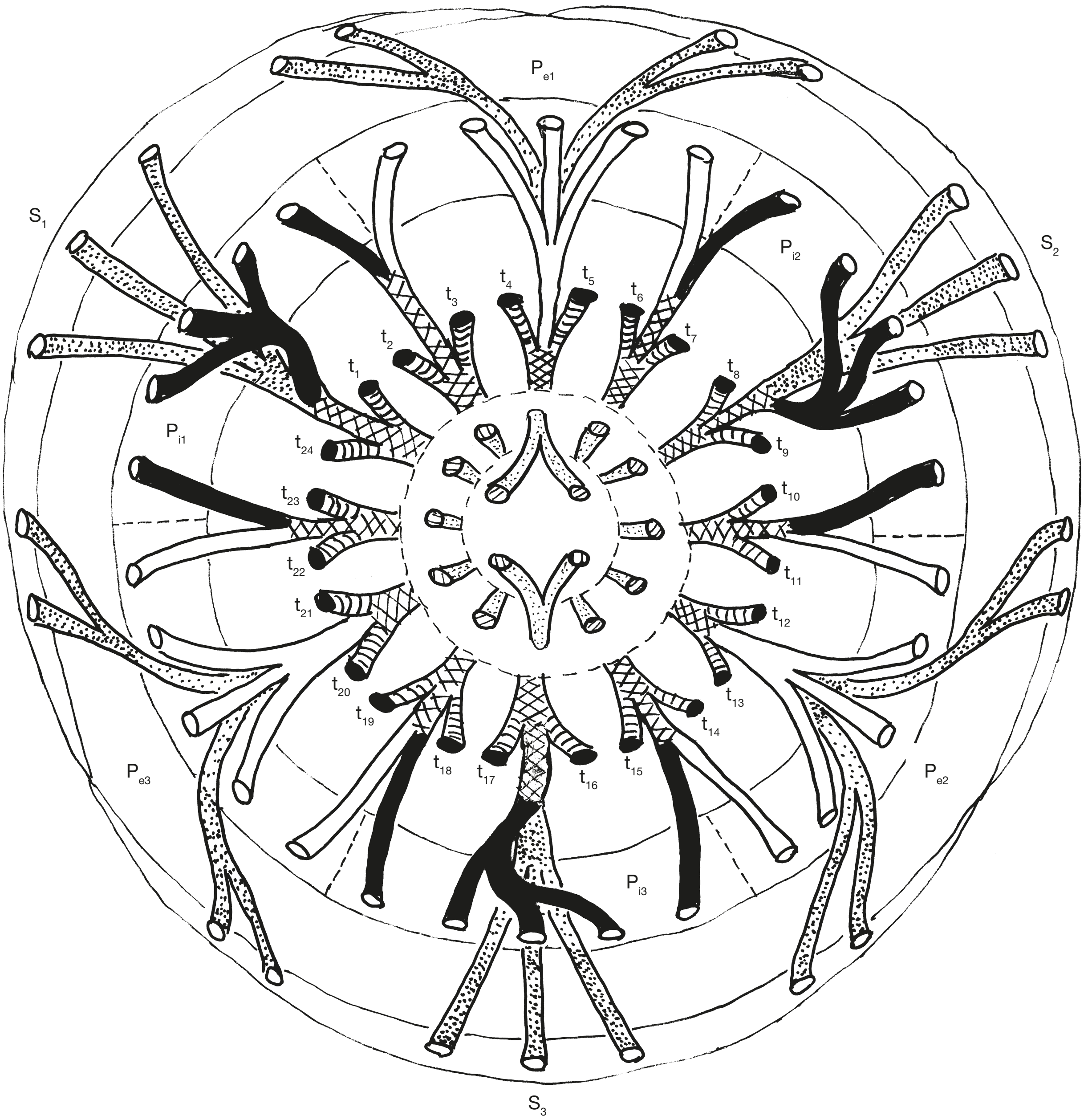

Fig. 5. — Vascular diagram of the flower of *Annona haematantha* Miq., sepal bundles stippled, outer petal bundles white, inner petal bundles black, stamen bundles hatched with black tips, carpel bundles stippled with hatched tips, fused bundles (cortical vascular system) crossed. Abbreviations: see Figures 2 and 3. Drawing: Thierry Deroin.

in the previously studied *Annona* species) and carpels (14 vs often much more in other species).

This type of gamopetaly was also documented in the African genus *Monodora* Dunal (Deroin & Couvreur 2009), where the petals are basally fused into a short tube, and the lateral vascular bundles are fused into synlaterals, but the petals are nevertheless differentiated above into inner and outer petals.

Annona ambotay Aubl. is suggested to be closely related to *A. haematantha* (Maas *et al.* 2007). Preliminary unpublished phylogenetic data indeed suggest that they are sister species, forming a clade with a yet undescribed *Annona* species. We did not study either of these other species here, but based on photographic material both show a similar floral structure to *A. haematantha*, and we can thus hypothesize that they have a similar vasculature.

Besides vasculature anther and gynoecium histology was also observed. As usual in Annonaceae, anthers exhibit a varied histology, remarkable here by a reddish dense tissue and huge secretory cells. It is noteworthy that the extrorse character and relative size of pollen sacs increase with the level of section, even tissues distribution may differ. A comparative anther histology in Annonaceae should take in account such an intrastaminal variation. Anther histology and outline are very like those described for *Annona squamosa* L. and above all *A. senegalensis* Persoon (Deroin 1988a: 59-60, pl. 25) but their conducting bundle is there amphihloic, thus expressing the diplophyllous character of the stamen, result of the congenital fusion of two inverted laminas (Deroin 1991). Conversely the phloem-xylem bundle of *A. haematantha* is collateral (Fig. 5) – i.e., diplophylly is fading – and thus appears as more advanced in the genus (Deroin 1991).

Finally, the gynoecial architecture conforms wholly to the classical pattern described for *Annona* (Lyagalwar 1979, Briechle-Mäck 1994). The range of carpel numbers in Annonaceae is generally reported in taxonomic studies, but are in some cases hard to count at the morphological level, and are thus in some cases unreliable. For example, anatomically, we observed in the studied flower 14 carpels in our specimen of *A. haematantha*, but Maas *et al.* (2023) recently quoted 25-30 carpels for the species.

In addition, we observe that the inner petals are not tightly appressed to the reproductive organs in *Annona haematantha*, suggesting a wide floral chamber for potential pollinators to move around. Pollination chambers have been defined in Annonaceae as "formed from a corolla tube that results either from basal fusion of petals or free petals" (Saunders 2010, 2012; Sauquet 2016). Saunders, in a review of Annonaceae flower evolution (Saunders 2010), classified Annonaceae pollination chambers into seven different types (I-VII). Based on this, *A. haematantha* would fit in Type VII: "Pollination chamber formed from a corolla tube that results either from basal fusion of free petals". Indeed, the petals, inner and outer, are not connivant *per se*, but are loosely contiguous, not touching and erect and rigid. In this type VII pollination chamber, access to the chamber is probably limited by the inner petals applying a filter against large beetles, thus favoring smaller ones. One can hypothesize that fusion of the inner and outer petal whorls reinforces this filter as access to the chamber is only possible from above. The genus *Annona* was suggested to have a range of pollination chamber types (at least four different ones), but not the type VII (Saunders 2010). Type VII is reported for species in the African genus *Isolona* Engl. and South American *Hornschuchia* Nees which also show a fused tube at the base with erect petals (Couvreur 2009; Johnson & Murray 1995). This suggests an independent evolution of this character across the evolution of Annonaceae pollination strategies in the family (Saunders 2010). As indicated above, a few other species of *Annona* show this morphology (i.e. *A. ambotay*), and they form a single same clade (unpublished phylogeny). Thus, within *Annona* this type VII pollination chamber might have evolved a single time. Over all, our results reinforce the observation that *Annona* species show a wide floral morphological variation (Rainer 2007; Maas *et al.* 1992).

Another interesting observation is related to the nectaries found in the inner petals. As far as we can tell, the presence of prominent nectaries at ¾ of the inner petal length, just below the tips, in *Annona haematantha* is remarkable in *Annona* as they are usually found as a flat red smear at their concave base, like in *A. muricata* or *A. senegalensis,* and even at the base of outer petals where inner ones are lacking (*A. squamosa* (Deroin 1988a). The same pattern was described in *Cananga* (Dunal) Hook.f. & Thoms. (Deroin 1988b). In *Isolona*, the red patch is annular and spreads along the petal tubes (Deroin & Couvreur 2009). Some Annonaceae genera have their nectaries along the margins of the inner petals, such as *Monodora* and *Orophea* Blume. However, in the case of *Annona haematantha*, the inner petals appear to be wholly and deeply modified in their upper section into true glands. This may seem illogical when it comes to rewarding pollinators but as the inner petals are bent towards the inside of the flower (Fig. 7A-C), pollen and reward are brought closer. Could it be that nectary glands close to the inner petal tips is more frequent that currently known, especially in species presenting a floral chamber? The location and development of the nectary glands should be described in the field, during the different anthetical stages, because they are hardly recognizable in herbarium specimens. Recent studies demonstrate that a wide range of habit, vegetative and reproductive characters, pollination syndromes, flowers and fruit anatomy occur in Annonaceae, but our knowledge remains very patchy so that no comparative synopsis of these relevant features might be proposed (as for other Magnoliales and Winteroids). In fact, it would be beneficial to study thoroughly the histology, histochemistry of these areas, and their accurate cytology by transmission electron microscopy.

A rather similar glandular tissue was described in the Chinese *Alphonsea glandulosa* Y.H. Tan & B. Xue by Xue *et al.* (2017), and such a corrugated gland also occurs in the Gabonese genus *Pseudartabotrys* Pellegr. but with a lipidic content (Deroin & Bidault 2017).

Starch grains were revealed in the inner petals of *Annona haematantha*, a known substance used by plants to generate heat, which is favourable for attracting nocturnal pollinators, a common feature of flowers pollinated by small and large beetles (Gottsberger & Webber 2018). Finally, the presence of curled hairs on the inside of the inner petals could constitute an obstacle to an early exit of the floral chamber by the pollinators.

Our study highlights an interesting flower morphology in *Annona*, probably shared with its sister species to *A. ambotay* and an undescribed species, all three forming a clade in *Annona* (results not published). More studies are required to compare species of this clade. In addition, pollination studies could also bring insights into what insects pollinate this type of flower, considering that the prominent nectary glands located near the tip of the inner petals, represent most probably an adaptation to specific pollinators.

As mentioned earlier this study was initiated when the first author (CRV) came across an unusual description of the corolla of *Annona haematantha* while entering morphological data in PROTEUS. The importance of the so-called Big Data in science is now evident with long hours spent computing the data and analyzing it in a variety of fields of science. The invalid, approximate, or erroneous data entered in such large databases can stay unquestioned and unchecked for a while, if ever. Even if a couple of errors have little impact on the conclusion of large-scale studies, this study shows that when puzzling data is found, its investigation may reveal something unexpected.

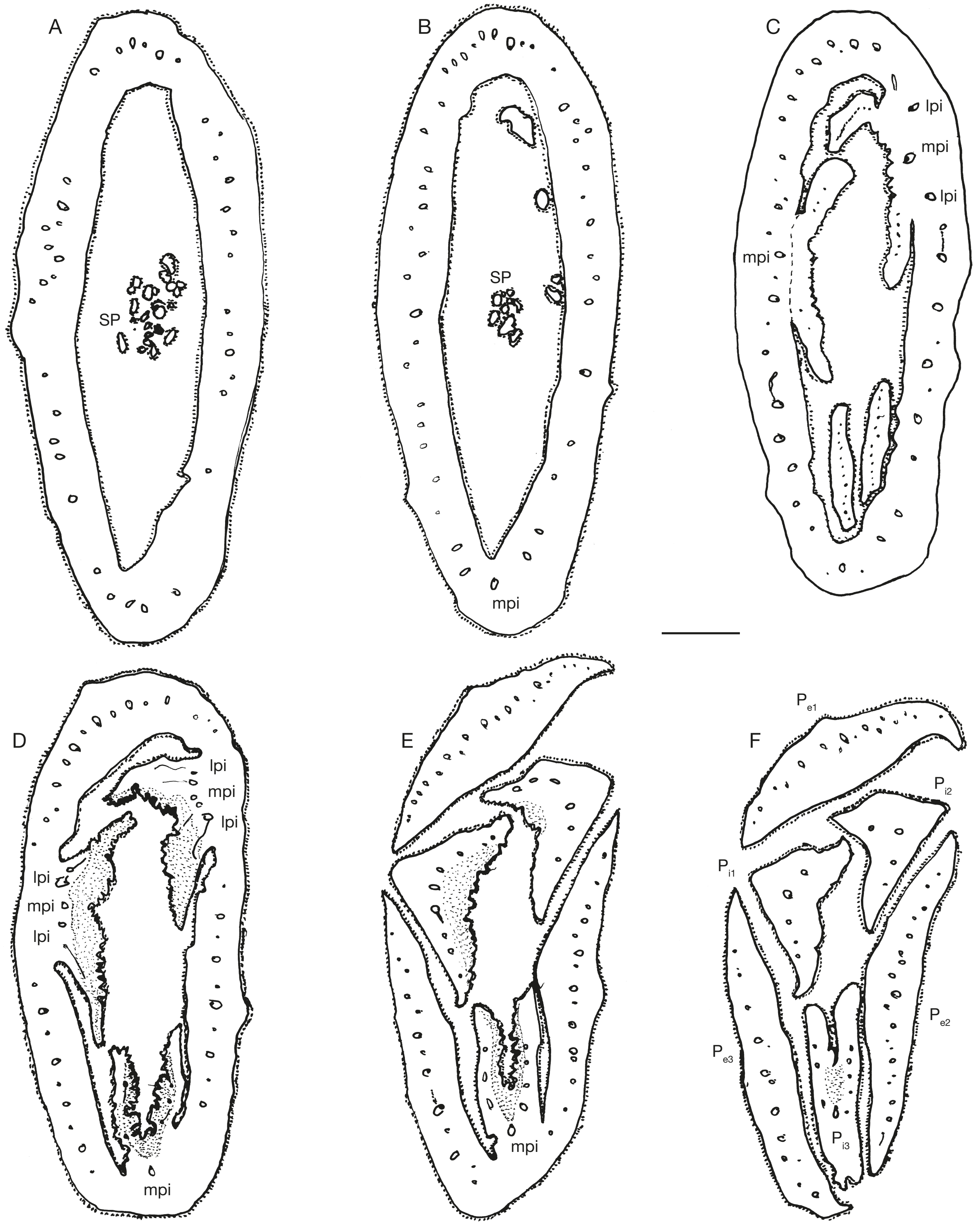

FIG. 6. — Transverse ascending sections of the corolla of *Annona haematantha* Miq., tube zone (**A**, **B**) with the top of stigmatic plate. Secretory zone (**C**-**E**) with inner petals modified into glands; apical zone (**F**) with classically arranged petals. Abbreviations: **lpi**, lateral bundle of inner petal; **SP**, stigmatic plate; other abbreviations: see Figs 2 and 3. Drawings: Thierry Deroin. Scale bar: 1 mm.

Combining all the above anatomical and morphological observations it is possible to propose an informed hypothesis concerning the type of pollinators more likely to visit the flowers of *Annona haematantha* and the species' pollination syndrome. Following Gottsberger & Webber (2018), multiple characters found in the flower of *Annona haematantha*, as well as field

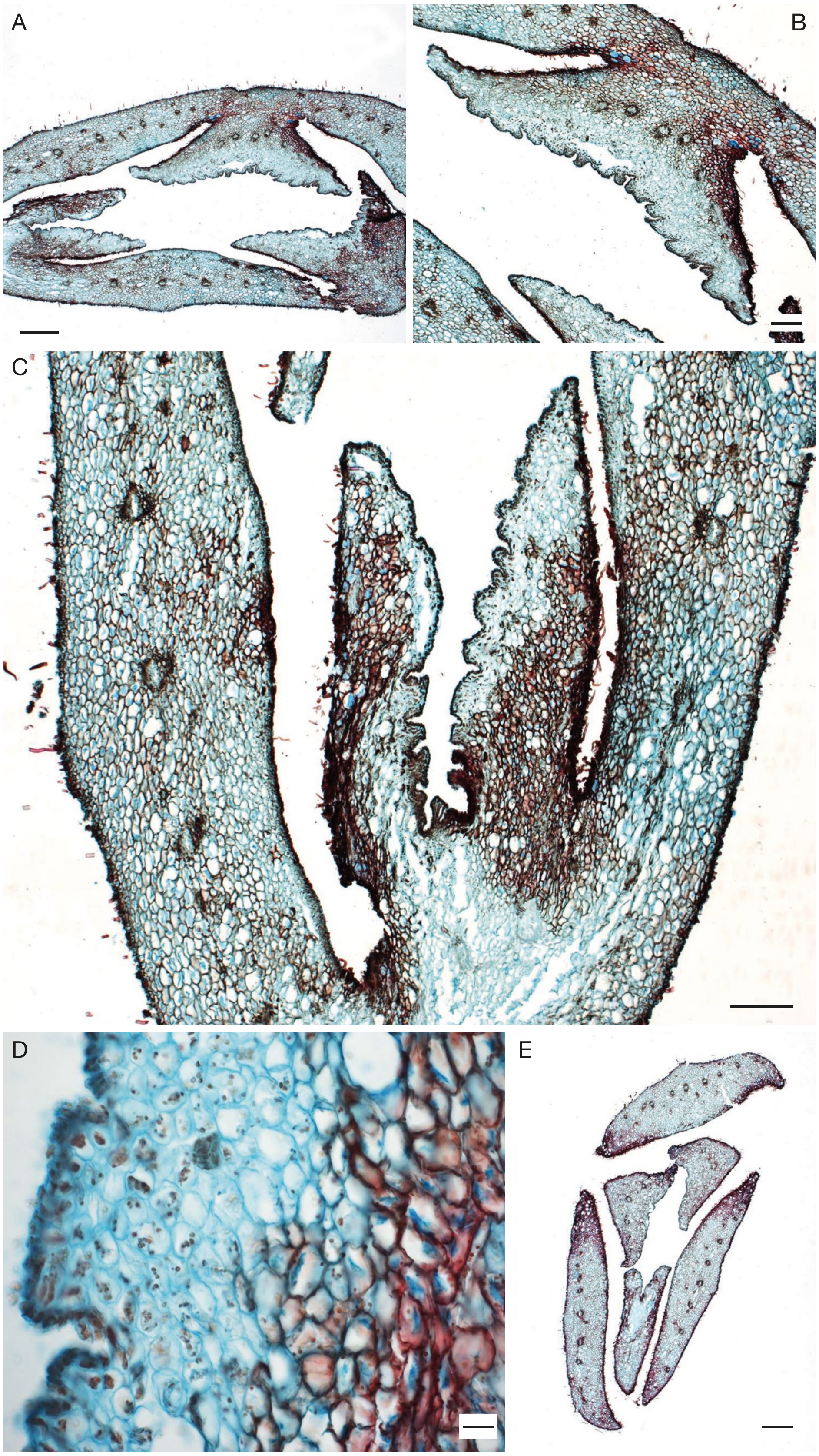

Fig. 7. — Details of secretory tissues in the inner petals of *Annona haematantha* Miq.: **A**, **B**, insertion of the inner petal in the corolla and vascularization; **C**, cross section of the inner petal modified into a bifid corrugated gland; **D**, close up on the secretory tissue, note the numerous starch grains (stained in red by Fuchsine); **E**, apex of the corolla showing the usual annonaceous pattern. Photos : Isabel Le Disquet. Scale bars: A, E, 500 µm; B, C, 200 µm; D, 20 µm.

notes on the label of *S.Mori & B. Boom 14754*, suggest that this species is pollinated by nocturnal small beetles, and not large ones linked to the function of the inner petals. These characters are as follows: small flowers, thickened outer petals, starch grains (enabling thermo-genesis), presence of hairs, inward-curling, curved inner petals but with the apex bent outwards forming a small entrance, and likely scent emission. All these features should be of course checked in the field.

Could the nectary glands located near the tips of the inner petals be another character common in species pollinated by small (or maybe also large) beetles in flowers with floral chambers? This might just be a unique feature of *Annona haematantha* flowers. Only more anatomical studies will enable us to answer this question.

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