

# Floral anatomy of *Pseudartabotrys* Pellegrin (Annonaceae), a monospecific genus endemic to Gabon

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## ABSTRACT

Floral anatomy of the monotypic Gabonese genus *Pseudartabotrys* Pellegrin was studied, in order to get a better understanding of the origin of pseudosyncarpy and its morphological context. Receptacle vasculature is moderately advanced with a partial perianth cortical vascular system, however much less developed than that of *Annona* L. Anther histology is complex, with a thick hypodermal sclerenchyma on the abaxial side, reminiscent of that previously recognized in *Uvaria scabrifida* Oliver, whose fruit resembles a pseudosyncarp. Gynoecial anthotaxy, 1 (2)-ovulate carpels and an outer compitum foreshadow the pseudosyncarpous fruit. Androecial and gynoecial vasculatures are free and both trimerous and pentamerous, following the likely basal condition in Magnoliales. A new kind of food body for the Annonaceae, found at the adaxial concave base of the inner petals, epidermal in origin with a lipidic spongy frame and showing no direct connection with venation, is briefly described. We emphasized the significance of classical approaches in the study of endemic and possibly endangered taxa, which are often revealed to be critical in the understanding of biological evolution, both by the primary data obtained and by the field and experimental researches they further suggest, in comparison with more widely distributed taxa.

## KEY WORDS

Annonaceae,  
cortical vascular system,  
Duguetia clade,  
floral anatomy,  
food bodies,  
pseudosyncarpy.

## RÉSUMÉ

*Anatomie florale de Pseudartabotrys Pellegrin (Annonaceae), un genre monospécifique endémique du Gabon.* L'anatomie florale du genre gabonais monotypique *Pseudartabotrys* Pellegrin a été étudiée, afin de parvenir à une meilleure compréhension de l'apparition de la pseudosyncarpie et du contexte morphologique associé. La vascularisation du réceptacle est médiocrement avancée, avec un système cortical partiel, beaucoup moins étendu que celui des *Annona* L. L'histologie de l'anthere est complexe, avec un épais sclérenchyme d'origine hypodermique sur la face abaxiale, rappelant celui précédemment vu chez *Uvaria scabrifida* Oliver, dont le fruit évoque d'assez près un pseudosyncarpe. L'anthotaxie du gynécée, les carpelles 1(2)-ovulés et le compitum externe formé par un capuchon muqueux préparent le fruit pseudosyncarpique réalisé à maturité. Les vascularisations de l'androcée et du gynécée sont libres et à la fois trimères et pentamères, selon la condition probablement ancestrale dans les Magnoliales. Un type de corps nourriciers, nouveau pour les Annonaceae, est reconnu et brièvement décrit à la base concave adaxiale des pétales internes, il est d'origine épidermique, avec une trame lipidique alvéolaire et sans lien direct avec la nervation. Nous soulignons l'intérêt d'une approche classique de taxons endémiques, parfois menacés, qui se révèlent souvent cruciaux dans la compréhension d'une phylogénie, tant par les résultats primaires obtenus, que par les recherches de terrain et les expériences futures qu'ils inspirent, en regard de taxons plus largement répartis.

## MOTS CLÉS

Anatomie florale,  
Annonaceae,  
clade *Duguetia*,  
corps nourriciers,  
pseudosyncarpie,  
système vasculaire  
cortical.

## INTRODUCTION

Annonaceae is a large pantropical family, identified as a homogenous entity since the very beginning of plant classification and the publication of Jussieu's (1789) *Genera Plantarum*. Though it is not, in terms of number of species, the richest family in Angiosperms, it is the most diverse among Magnoliales (Keßler 1993). With around 2400 liana, tree and shrub species, in 108 genera (Chatrou et al. 2012; Rainer & Chatrou 2017), Annonaceae greatly contribute to the floral diversity of intertropical forests at global scale (Gentry 1993; Tchouto et al. 2006; Punyasena et al. 2008).

In 1920, François Pellegrin described his new genus *Pseudartabotrys* as being related to the genus *Artabotrys* R.Br. by its petals, and much closer to *Cyathocalyx* Champ. ex Hook.f. & Thomson, but distinctly differing from it sharply by the gynoecium pattern, whose carpels are sunken in the receptacle and connate as seen in some *Annona* species: "voisin du genre *Artabotrys*; par ses pétales, [et] encore plus voisin du genre *Cyathocalyx*, mais il en diffère nettement par l'organisation du gynécée, dont les carpelles sont immergés dans le réceptacle et connés comme cela se rencontre chez certains *Annona*". Unfortunately, no mature fruit was yet observed at this time. Pellegrin (1920) recognized a unique species: *Pseudartabotrys letestui*, based upon a single gathering by Georges Le Testu, in the Mayombe Bayaka, Gabon (*Le Testu 1432*, Moabissako, dans une gorge humide et resserrée sur la route de Massanga à Moabissako, fl., 22.X.1908; holo-, P[P00363397]; iso-, BM, P[P00363395, P00363396]).

During more than 90 years, few advances were made in the morphological knowledge of *Pseudartabotrys*. A plate was published in an additional note (Pellegrin 1924), the genus being further included in the classical monograph of Annonaceae by Fries (1959: 122) who considered it in his "Artabotrys-Gruppe", linked to seven other genera: *Artabotrys*, *Cyathocalyx*, *Disepalum* Hook.f., *Drepananthus*

Maingay ex Hook.f., *Enantia* Oliv.(= *Annickia* Setten & Maas), *Marsyopetalum* Scheff. and *Neostenanthera* Exell. In her contribution to the Flore du Gabon (1969), Le Thomas provided much more details about the habit, vegetative and floral morphology of this genus and also examined it in her comparative palynological study of Annonaceae (Le Thomas 1980, 1981), strengthening – by its distal exine with a discontinuous outer layer and a foliated basal layer – a relationship with *Letestudoxa*, and even showing a striking analogy with the paracarpic genus *Isolona* Engl. The genus was treated in a comprehensive study of floral morphology in Annonaceae (van Heusden 1992: 82), and then assigned to a *Fusea*-group including six other genera: *Afroguatteria* Boutique, *Disepalum*, *Duckeanthus* R.E. Fries, *Enicosanthellum* N.T. Ban, and *Fusea* (Baillon) Safford.

It should be noted that Pellegrin in his seminal paper of 1920 did not put together *Pseudartabotrys* with *Letestudoxa*, the next genus he described, but compared the second to *Pachypodanthium* Engl. & Diels (= *Duguetia* A.St.-Hil., after Chatrou et al. 2012). His intuitions were brilliantly confirmed by the recent phylogenetic studies of Couvreur et al. (2011) and of Chatrou et al. (2012) in which these two genera may be placed in a *Duguetia* clade with *Artabotrys*, *Duguetia*, *Fusea* Saff., and *Xylopia* L., thus also supporting in part the previous proposal of van Heusden (1992).

The first fruiting specimen was collected more than sixty years after the description of the species (*de Wilde et al. 890*, 3.III.1983, Wonga-Wongué Reserve) revealing pseudosyncarpy and a persistent calyx. The species has regularly been collected since, and photographed once (*Wieringa & van Nek 3273*, Doudou mountains, 24.XI.1994 [WAG0158167]). Although many flowering specimens have been collected during the 80's and 90's, the second author made a recent collection (*Bidault 1693*, 7.X.2014, M'paga prefecture, 7 km North of Lake Alombié), and had the opportunity to gather multiple flowers preserved in spirit.



FIG. 1. — Flower of *Pseudartabotrys letestui* Pellegrin in live: **A**, **B**, old and younger anthetic flowers at ♀ stage; **C**, detail of **A** from below, note the central stigmatic plate covered by mucilaginous cap and immature stamens with pink connective heads; **D**, flower just after fertilization: all petals, stamens and stigmas are fallen, while sepals remain patent in the maturing fruit. Photos by Ehoarn Bidault, linked to *Ehoarn Bidault 1693* (P00854827).

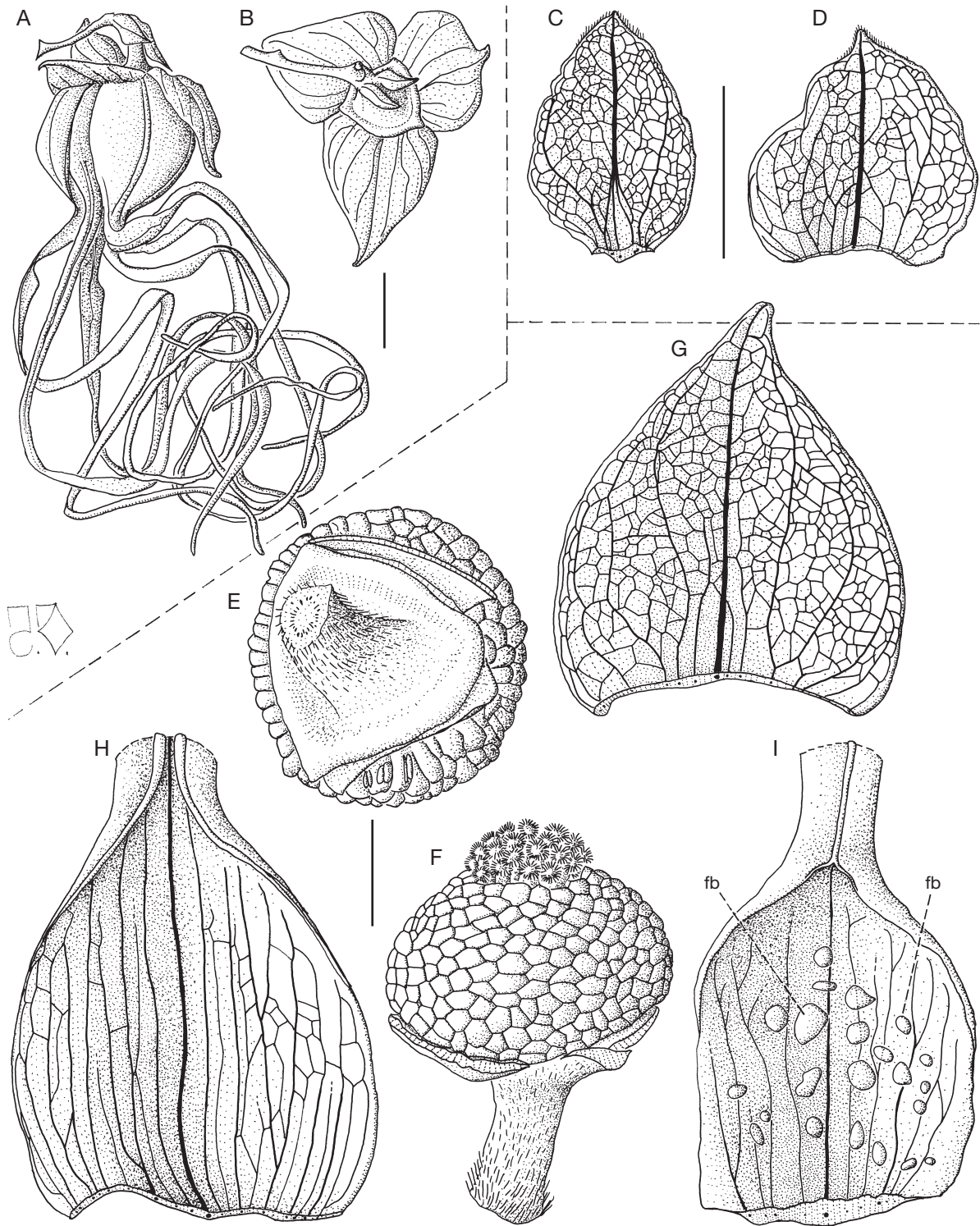


FIG. 2. — Morphological details of the studied flower of *Pseudartabotrys letestui* Pellegrin (*Ehoarn Bidault 1693*, P[P00854827]): **A**, side-view of the anthetical flower (female stage); **B**, basal view showing pedicel, bracts and calyx; **C**, **D**, lower and upper bracts; **E**, **F**, basal and side views of androecium and gynoecium on the receptacle, perianth removed; **G**, sepal; **H**, base of outer petal; **I**, base of inner petal, **fb**: food body (all in ventral view). Scale bars: A, B, 1 cm; C, D, E-I, 5 mm.

It seemed advisable to acquire more detailed data about the floral anatomy of such a scarce genus, seen as a living treasure of Gabon, in order to further improve our understanding of the Annonaceae family, especially the emergence of pseudo-syncarpic/syncarpic clades.

#### MATERIAL AND METHODS

A unique flower at anthesis (Gabon, *Ehoarn Bidault 1693* [P00854827], female stage; Fig. 1) was fixed in the field by FAA, then preserved in a mixture of glycerol/water/etha-

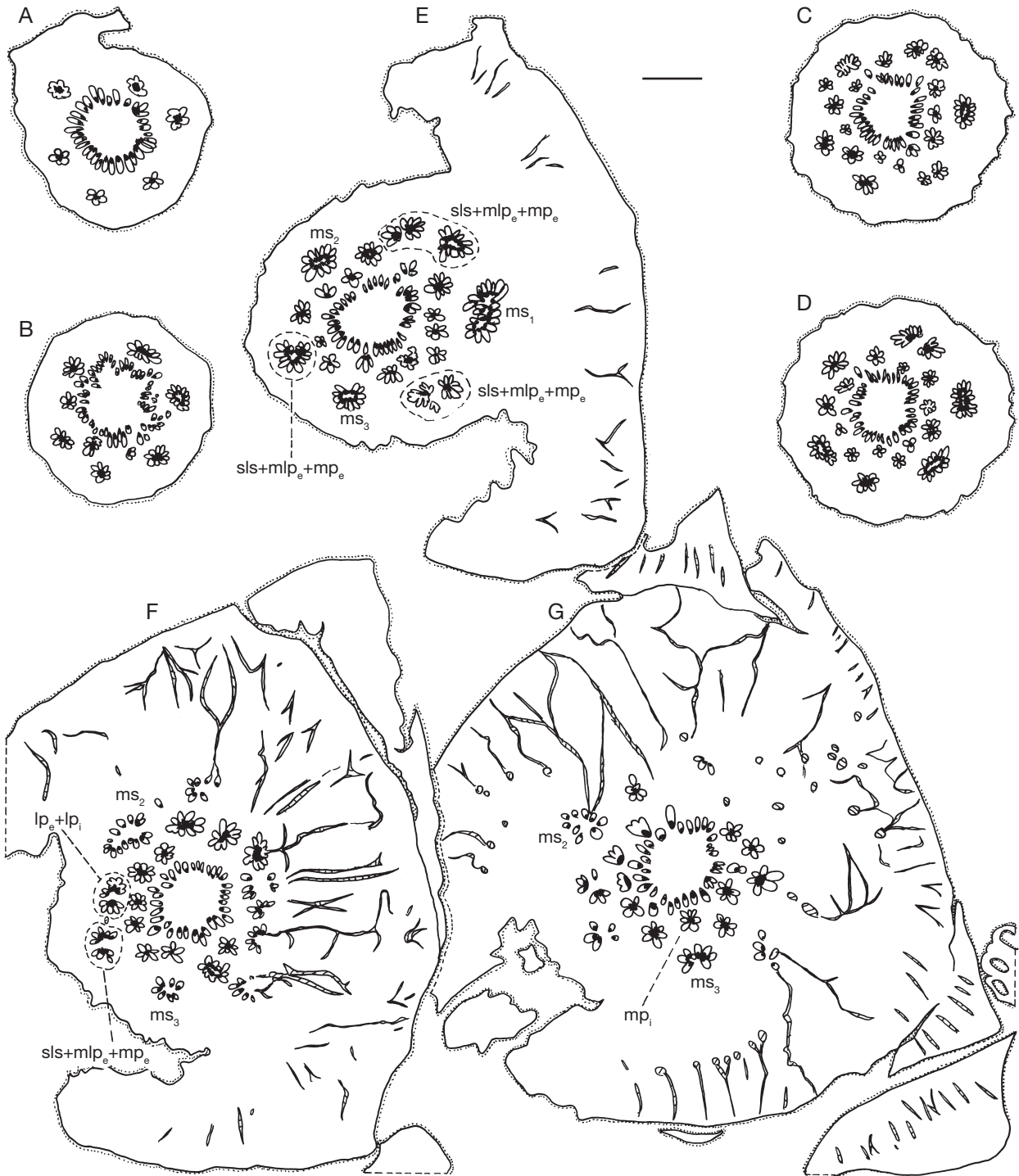


FIG. 3. — Ascending transverse sections of the flower of *Pseudartabotrys letestui* Pellegrin: **A**, top of the pedicel; **B-E**, base of receptacle; **F, G**, at the calyx insertion level. Abbreviations: **lp<sub>e</sub>**, lateral bundle of outer petal; **lp<sub>i</sub>**, lateral bundle of inner petal; **mlp<sub>e</sub>**, mediolateral bundle of outer petal; **mlp<sub>i</sub>**, mediolateral bundle of inner petal; **mp<sub>e</sub>**, median bundle of outer petal; **mp<sub>i</sub>**, median bundle of inner petal; **ms**, median sepal bundle; **sls**, synlateral sepal bundle. Scale bar: 1 mm.

nol. After a partial dissection removing bracts and perianth parts, the flower was soaked in ethylenediamine 4% aq. for a week in order to soften hard tissues (Carlquist 1982), then dehydrated in a t-butanol series (Gerlach 1984) and infiltrated in paraffin (Histomed, melting point: 60°C). Basal parts of sepal, outer and inner petals were cut at 25 µm thick, and sections then stained by Astrablue [Chroma® 1B

163] 0.5% aq. and Ziehl's fuchsine [RAL® 320490-1000] 10% aq. Some sections of inner petal were processed by Lugol (and examined in it) for making starch conspicuous, others by Sudan IV [Chroma® 1A 262] and mounted in Agave syrup for lipids. Microtome sections were made at a thickness of 50 µm, but were not subject to staining as the presence of tannins made this step superfluous. All slides

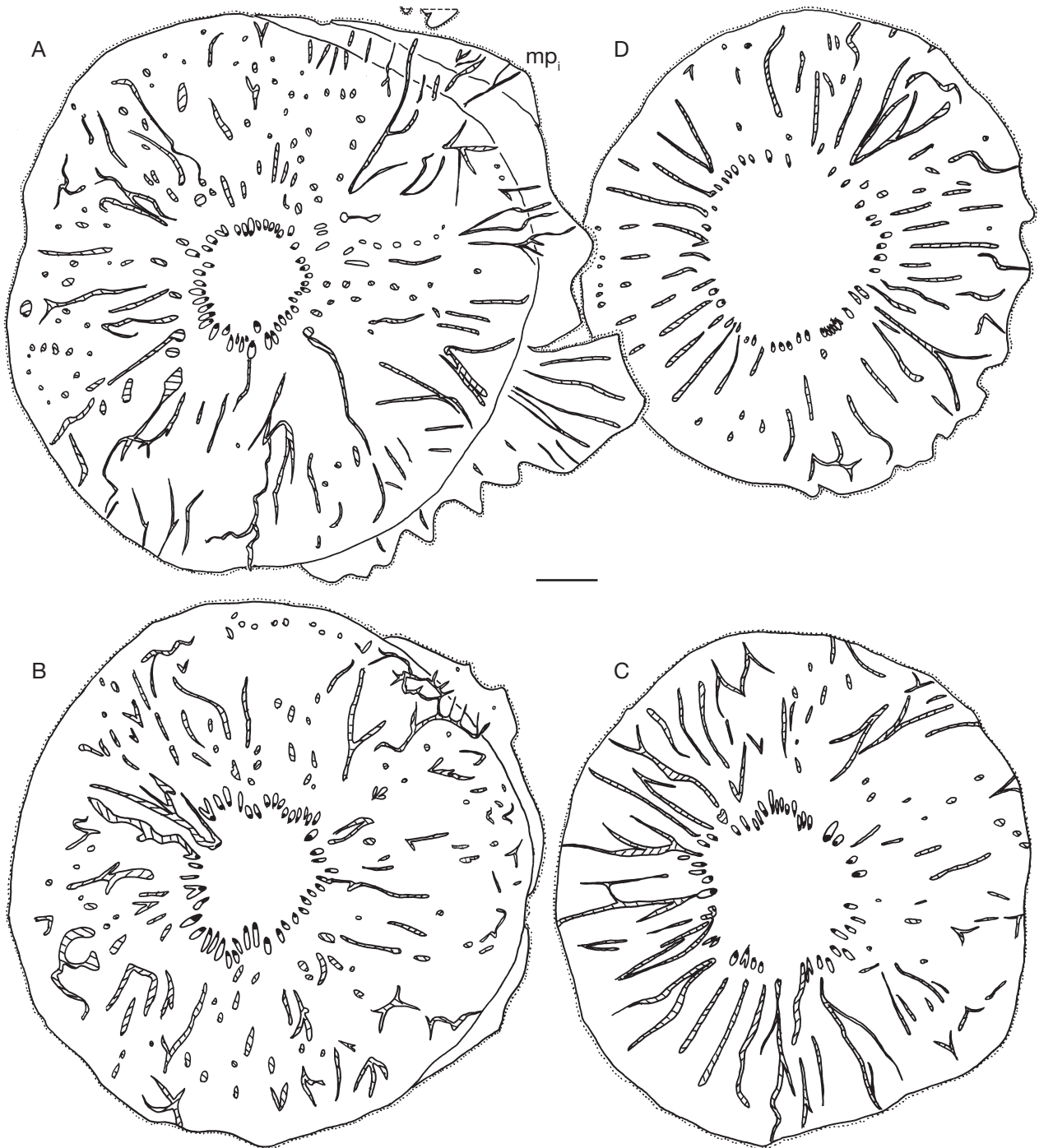


FIG. 4. — Ascending transverse sections of the flower of *Pseudartabotrys letestui* Pellegrin (continued): **A, B**, at the corolla insertion level; **C, D**, at the androecium insertion level. Scale bar: 1 mm.

were mounted in Eukitt [O.Kindler GmbH® E0214]. Slides are kept in the plant histological collection of the Muséum national d'Histoire naturelle, Paris, under the range reference *Deroin 227*.

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

## RESULTS

### ADDITIONS TO FLORAL MORPHOLOGY

Bract numbers are obviously uneasy to count in a too narrow sample. In her Gabon flora treatment, Le Thomas (1969: 316) described a single bract on the holotype, whereas we were able to distinguish two bracts (Fig. 2C, D), in some recent sheets

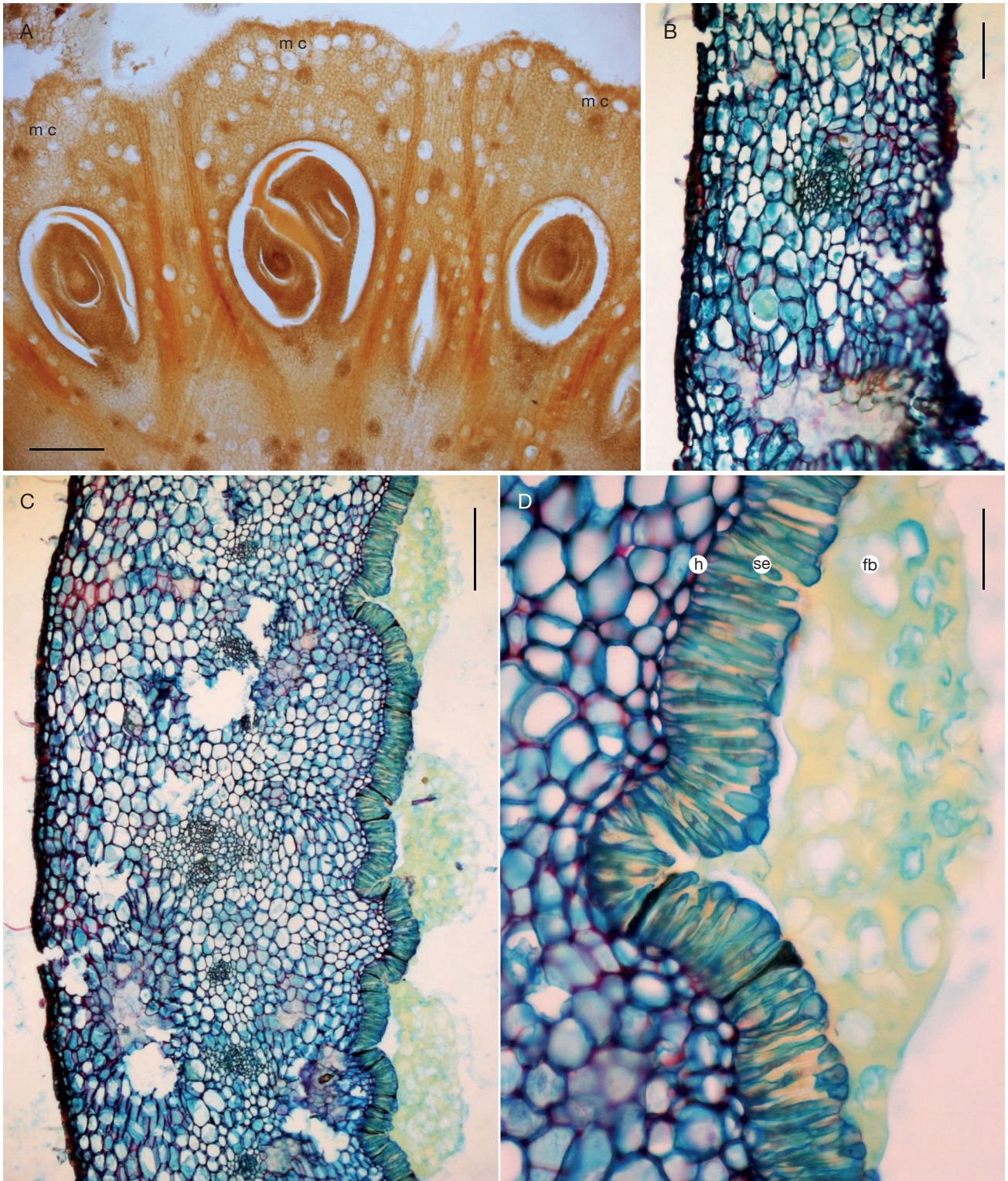


FIG. 5. — Histological details of floral organs in *Pseudartabotrys letestui* Pellegrin. Gynoecium: **A**, three peripheral carpels, note the biovulate central carpel. Petal bases in cross section: **B**, outer petal; **C**, **D**, inner petal and detail of a food-body. Abbreviations: **fb**, food body; **h**, hypodermis; **mc**, median carpel bundle; **se**, secretory epidermis. Scale bars: **A**, **C**, 200  $\mu$ m; **B**, 100  $\mu$ m; **D**, 50  $\mu$ m.

(e.g. *Wieringa & van Neck* 3273, WAG [WAG0158167]), three bracts were observed. In outline and venation, the bracts are rather like the sepals.

RECEPTACLE VASCULATURE (FIGS 3-5; 9)

In cross-section, above the upper bract but below the level of calyx insertion, the pedicel exhibits a stele made of *c.* 38 bun-

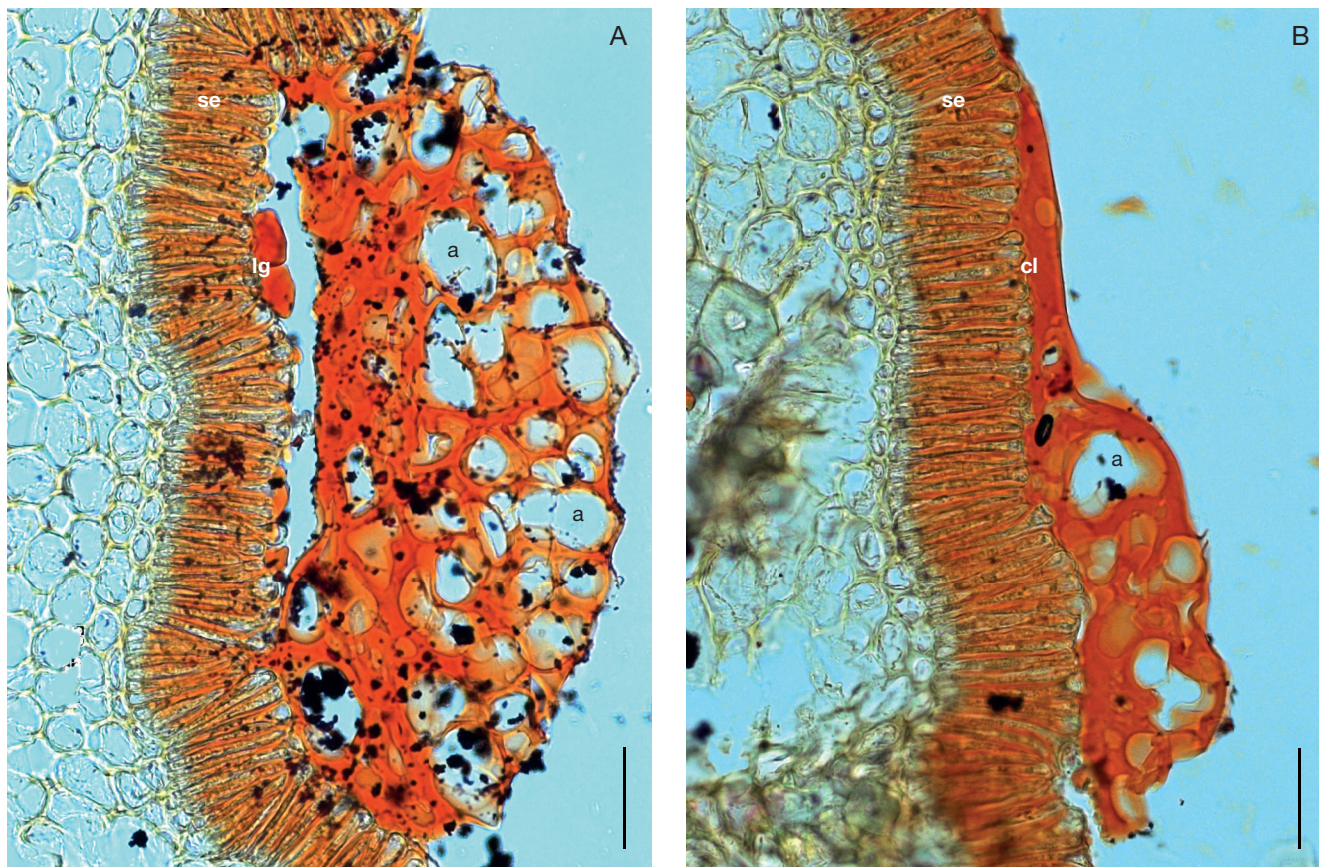


FIG. 6. — Details of food bodies at the adaxial base of inner petal, cross section stained by Sudan IV, in *Pseudartabotrys letestui* Pellegrin: **A**, median region; **B**, marginal region. Abbreviations: a, alveolus; cl, continuous lipidic layer; lg, lipidic globules; se, secretory epidermis. Scale bars: 50  $\mu$ m.

dles, among which 6 break up at the receptacle base (Fig. 3A-E), into two crowns, the outer of 3 median sepal bundles (ms), the inner one of 3 synlateral sepal bundles fused with median outer petal bundles (sls + mp<sub>o</sub>). All of these strands build up cortical pseudosteles, more or less with pith, while at the same level *c.* 15 bundles emerge from the central stele, tightly related to the supply of the three inner petals, six of them are fused lateral traces of outer and inner petals and the nine others are separate mediolateral and median traces of the inner petals. These bundles are not medullated and branch in a very complex pattern (Figs 3F, G; 4A, B). Above the level of the corolla traces, *c.* 30 bundles emerge from the central stele (Figs 4C, D; 5A-C), constituting the vascular trunks of the androecium, each supplying *c.* 10 stamens (Figs 5B, C; 9[t]). We count 312 stamens for the whole flower. At the same level the central stele enlarges, breaking up into *c.* 45 minute bundles which feed the gynoecium. At anthesis, pith is wholly parenchymatous whereas some sclereids are scattered throughout the cortex.

#### GYNOECIUM

Eighty eight carpels are inserted at the top of the receptacle (Fig. 7E), loosely arranged in five whorls (we count 30, 23, 19, 11, 5 carpels toward the centre). Each carpel exhibits three traces (i.e., a median bundle, and two mediolateral ones

basically fused to lateral bundles). As a rule in the family, the median bundle supplies the ovule, which is here solitary, basal and erect. Two ovules were observed in one carpel (Fig. 5A), a feature recognized previously at the same lateral location in *Annona reticulata* by Briechle-Mäck (1994: 28, fig. 38), and otherwise frequent in the apical carpel of *A. muricata* (Deroin 1988a: vol. 2, 77, fig. 17). Carpels are strikingly elongated, resulting in a somewhat long stylar zone, an unusual feature in Annonaceae (except in *Anaxagorea* St.Hil., van Heusden 1992; Endress & Armstrong 2011).

The stigmatic plate belongs to the pattern “modèle compact” (Deroin 1991), very near the type 1 described by Briechle-Mäck (1994: 99) in which the mucilage cap secreted during the female stage creates an outer compitum (Endress 1982; see also Fig. 1C). As described by Le Thomas (1969: 316) the upper third part of the styles and stigmas is covered by long hairs, which are 1-celled and lignified, and at the apex of the stigma are scattered among the receptive papillate epidermal cells.

#### PETAL MORPHOLOGY AND HISTOLOGY (FIG. 5)

Petals differ mainly from the sepals by their abscission after anthesis and trend toward parallel venation and unifacility (exhibited by the inner petal). In outer petals (Fig. 5B), the blade is *c.* 380  $\mu$ m thick, with thin tanniferous epidermises



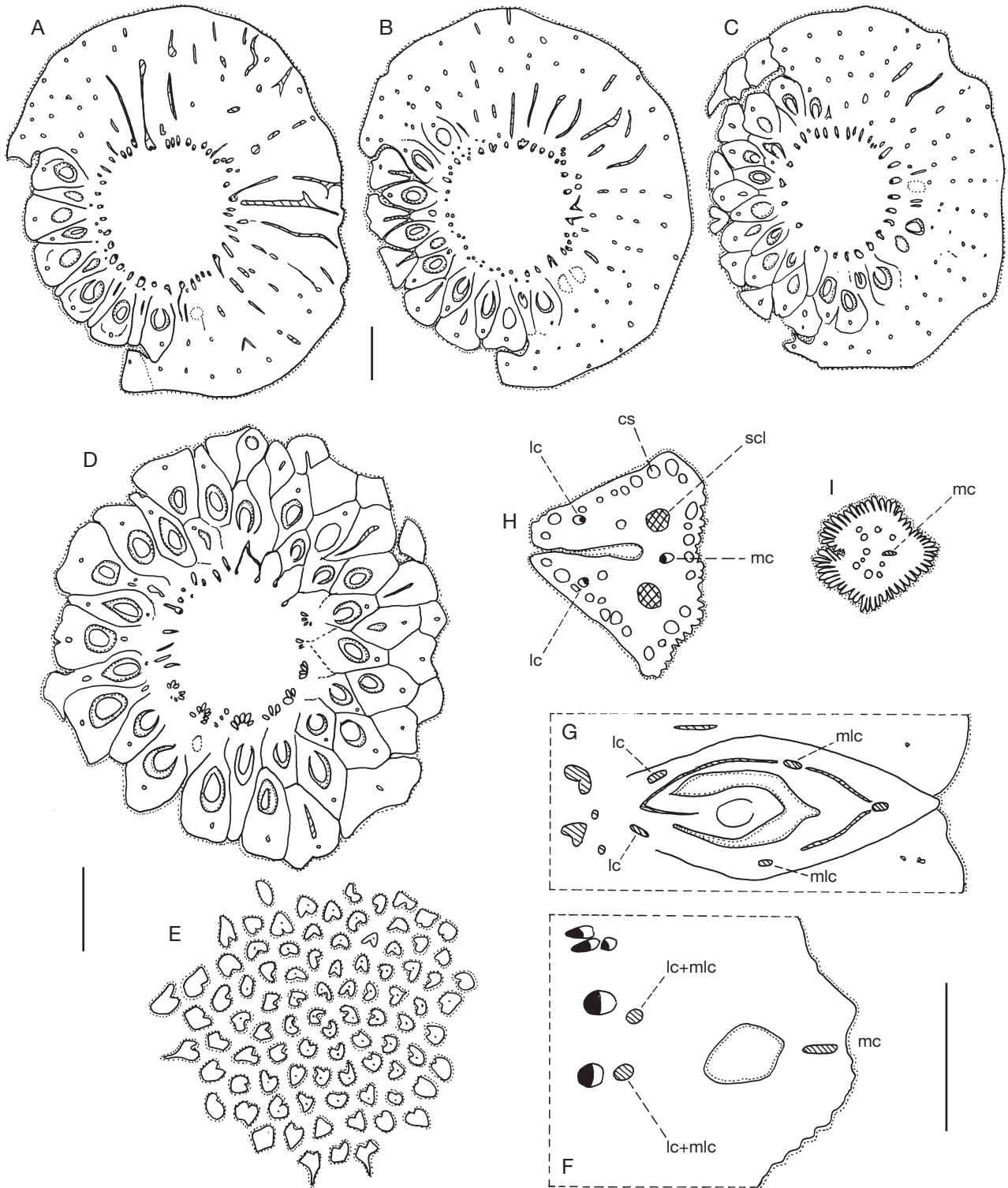


FIG. 7. — Ascending transverse sections of the flower of *Pseudartabotrys letestui* Pellegrin (continued): **A-C**, top of the receptacle exhibiting androecial vasculature and insertion of the lower carpels; **D**, mid-section of the gynoecium; **E**, stigmatic plate; **F-I**, detail of a carpel: basal vasculature, ovule supply, stylar zone and stigma. Abbreviations: **cs**, secretory cell; **lc**, lateral bundle of carpel; **mlc**, mediolateral carpel bundle; **mc**, median carpel bundle; **scl**, sclerenchyma. Scale bars: **A-C**, **D**, **E**, 1 mm; **F-I**, 500 µm.

(with short simple hairs) outlined by hypodermises, 14-17 layers of parenchyma cells, including some stone cells crowded in globular clusters, and venation occurring in the middle. Inner petals (Fig. 5C) have thicker blades (*c.* 890 µm, with 24-28

cell layers), with the structure of the abaxial side similar to that described for the outer petal in epidermal, hypodermal and parenchymatous zones (outer parenchyma *c.* 340 µm thick). Interestingly, short hairs are present at the adaxial side, but

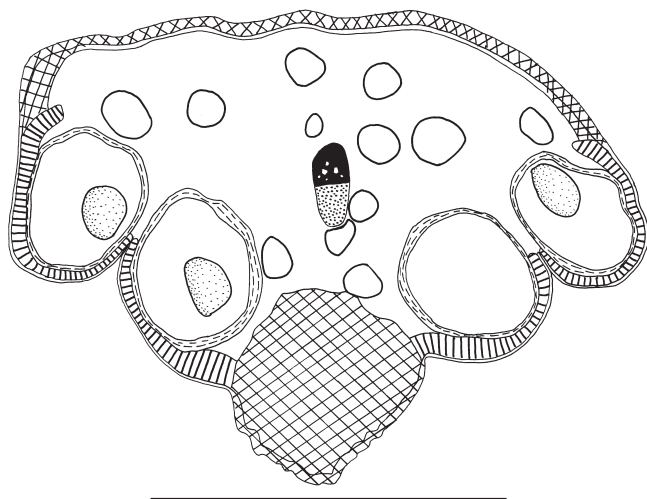


FIG. 8. — Anther anatomy of *Pseudartabotrys letestui* Pellegrin: **cross-hatching**, sclerenchyma; **hatching**, fibrous layer; **broken lines**, tapetum; **rings**, secretory cells; **stipple**, phloem; **black**, xylem. Ground parenchyma left in white. Epidermis and hypodermis delimited by two parallel lines. Floral center above. Scale bar: 500  $\mu$ m.

on a narrow strip near the margins only. Adaxial parenchyma is *c.* 420  $\mu$ m in thickness, and built by smaller and rounder cells. Venation is included in this inner parenchyma, just at the border of the outer (abaxial) one, while sclerenchymatous clusters are scattered throughout the whole blade. Adaxial hypodermis (Fig. 5D[h]) is cutinized 7–14  $\mu$ m high, and the adaxial epidermis is very thick (65–70  $\mu$ m), palisade-like and secretory (Fig. 5D[se]).

#### SECRETORY ADAXIAL EPIDERMIS (FIGS 5; 6)

Food bodies are obvious at the base of the adaxial side of inner petals (Fig. 2I[fb]), as ellipsoid “droplets” of 270–2000  $\mu$ m in diam. (mean value *c.* 900  $\mu$ m) and *c.* 150  $\mu$ m thick (Fig. 5C, D[fb]; 6A), showing a resinous consistency. These food bodies originate as small yellowish lipidic globules (stained in cherry red by Sudan IV; Fig. 6A[lg]), which are then fused into a continuous layer (Fig. 6B[cl]), and later exhibit a honeycomb structure with numerous alveoli (Fig. 6[a]), perhaps with a mucilaginous content, weakly stained by Astrablue in Fig. 5D, but poorly preserved by the FAA fixation.

#### ANTHER HISTOLOGY (FIG. 8)

Stamen morphology is characterized by the occurrence of a median pillar at the abaxial side connecting the base to the connective head. The epidermis is continuous and thin on the pollen sacs, much thicker and lignified around the connective and pillar. The hypodermis is 1-layered and parenchymatous on the adaxial side only, whereas at the corners near the fibrous layer it is 2–3-layered and lignified, and much more thickened for building up the core of the pillar. Sclereids are present exhibiting pitted walls with narrow lumen ( $\frac{1}{3}$  to  $\frac{1}{5}$  of the cell diameter). A fibrous layer is sharply distinct from the rest of the hypodermis: no intermediate cells were seen. At anthesis the tapetum is 2–3-layered with flattened cells. Pollen grains are free.

The anther connective contains abundant parenchyma, including large rounded secretory cells, crowned by smaller cells. The collateral bundle exhibits equal xylem and phloem, with the metaxylem V-shaped, 6–10 cells in cross-section, and often discontinuous.

#### DISCUSSION

Our study of the floral morphology and anatomy of *Pseudartabotrys* brought to the fore four interesting features:

1) The receptacle vasculature (Fig. 9) exhibits a regular trimerous pattern, with a perianth cortical vascular system (CVS) with wholly free median bundles in sepals as well as mediolateral and median bundles in inner petals, very similar to that previously recognized in *Piptostigma fasciculatum* (De Wild.) Boutique ex R.E. Fr. (Deroin 1989). This pattern is rather basal in the family (as confirmed by the rather high number of pedicel bundles: 38 (> mean value *c.* 30). Sepals and outer petals have basically 3 traces, while inner petals are fed by 5 traces. Androecial vasculature is trimerous too, as a rule in Annonaceae and Magnoliaceae, here with 30 trunks, wholly free, while they are partly or entirely fused to perianth bundles in *Monodoroideae* and *Annona* species respectively (Deroin 1989). All carpels, basically supplied by *c.* 45 vascular trunks, appear loosely arranged in whorls along an almost perfect arithmetic sequence of common difference 6: 30–24–18–12–6 – only 2 carpels are missing (in the two apical whorls where narrower space might prevent carpel development) – and thus reinforces gynoeceal trimery. The coexistence of trimery and pentamery, at least in reproductive region, was previously demonstrated in *Meiocarpidium* and *Magnolia* (Deroin 1987; 2010: 52), and is here yet recognizable in vasculature: it might be an ancestral feature in Magnoliales;

2) Nutritious tissues on the adaxial side of inner petals were reported in Annonaceae since at least 40 years ago and their role in pollinator attraction is now firmly established (Gottsberger *et al.* 1998). In most of the studied species they result from a thickening and tangential division of hypodermis as e.g. in *Cananga odorata* (Lam.) Hook.f. & Thoms or in *Alphonsea glandulosa* Y.H.Tan & B.Xue, where the epidermal layer is rather flat (Deroin 1988b; Xue *et al.* 2017), while it is sharply corrugated in *Duquetia riparia* (Silberbauer-Gottsberger *et al.* 2003). A new type is seen in *Pseudartabotrys* where hypodermis is thin while only epidermal layer is secretory, palisadic and producing spongy lipidic food bodies possibly enclosing mucilage and likely other soluble molecules in their alveoli. These droplets seem to be renewed during the presumably short female stage of the flower by new lipidic globules (Fig. 6A[lg]), coalescing further in a continuous layer (Fig. 6B[cl]), into which new alveoli appear. Underlying tissues are devoid of starch at anthesis (no reaction with Lugol), nerves are more numerous than in outer petals, but no vascular branch directly supplies the secretory cells as described in *Pseuduvaria froggattii* (F.Muell.) Jessup by Silberbauer-Gottsberger *et al.* (2003: 709). No information about anthocyanins occurrence at this level is available;

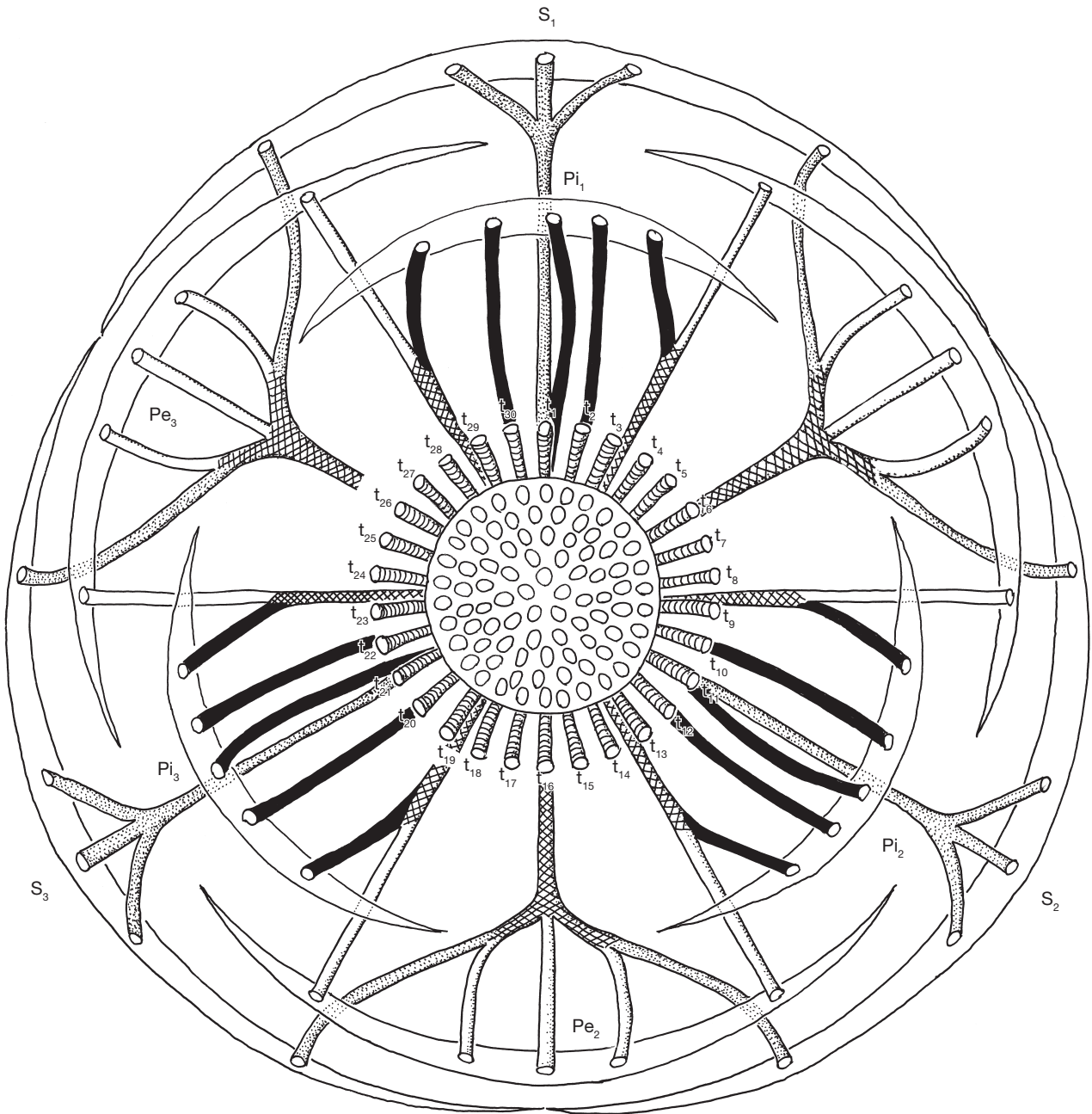


FIG. 9. — Floral vascular diagram of *Pseudartabotrys letestui* Pellegrin: **stippled area**, sepal bundles; **white area**, outer petal bundles; **black area**, inner petal bundles; **hatching**, stamen trunks; **cross-hatching**, cortical vascular system (CVS). Abbreviations: **P<sub>e</sub>**, outer petal; **P<sub>i</sub>**, inner petal; **S**, sepal; **t**, vascular stamen trunk.

3) Anther histology appears rather derived by its well distinguished fibrous layer inside the hypodermis without any intermediate cell as in e.g. *Meiocarpidium* Engler & Diels (Deroin 1987), as well as by the collateral bundle, and well developed sclerenchymatous abaxial pillar, which is an enlarged multilayered hypodermis. Such a feature is rather unusual in annonaceous stamens, but a similar structure is seen in *Uvaria scabrida* Oliver (Deroin 1988a: 55, pl. XXIV, 1), another West-African species, whose globular fruit of tightly clustered individual monocarps foreshadows a pseudosyncarp (Deroin 1999: fig. 5). These correlations between male and female structures should be accurately pinpointed and analysed in further studies;

And 4) The gynoecium is obviously pseudosyncarpous in structure, as confirmed by the mature fruit, which is strikingly similar to that of *Annona* (Fig. 10), even in the sporadic occurrence of some 2-ovulate carpels, but rather in a peripheral – as opposed to apical – location. The whorl of five central stigmas (Fig. 6E) is reminiscent of the two central almost fused styler zones in *Cananga odorata* (Deroin 1997) and strengthens the hypothesis that true paracarp – achieved in *Isolona* and *Monodora* – might originate by fusion of upper carpel regions inside pseudosyncarpous genera (*Duguetia* in the same *Duguetia* clade, *Annona* in the *Annona* clade), a hypothesis that is corroborated by recent

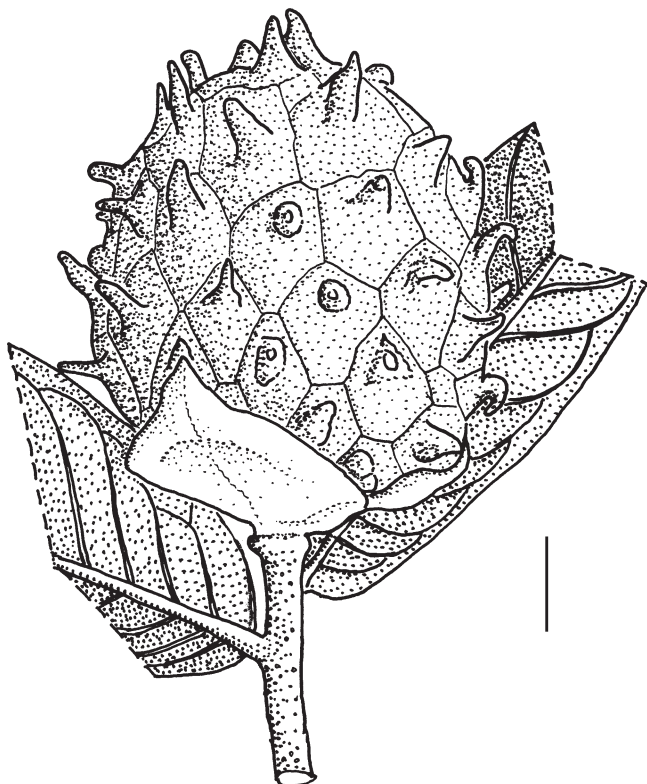


FIG. 10. — Fruit morphology of *Pseudartabotrys letestui* Pellegrin. Drawn after a field photograph of the specimen Wieringa & van Nek 3273 [WAG0158167]. Scale bar: 1 cm.

phylogenetic studies (Couvreur *et al.* 2008; Chatrou *et al.* 2012). Therefore, ontogenetically there may actually be no functional difference between congenital and postgenital syncarpy, the distinction resulting from the same morphogenetical process intervening at early versus late stages in floral development, and possibly correlated closely with the functional compitum.

## CONCLUSIONS

Our study of the *Pseudartabotrys* flower highlights the significance of static anatomical features (vascular architecture and histology) as the basis for undertaking any further research in morphogenesis, floral biology or fruit dispersal. Despite the apparent complexity and entanglement of the vasculature, a fundamental whorled architecture can be recognized, as in most magnolialean flowers (Deroin 2010).

The *Pseudartabotrys* flower shows – at anthesis – a combination of parts at different evolutive levels. Receptacle vasculature is moderately derived (CVS of weak extent), while the androecium and gynoecium are more specialized (stamens numerous with a varied histology; carpels numerous, 1-ovulate, postgenitally fused).

Finally food bodies on the adaxial side of inner petals appear as highly specialized structures inside a rather ordinary corolla (but upper part of petals is unifacial).

However it is necessary to link these secretory tissues to pollination biology, especially the foraging behaviour of pollinators. On the other hand, despite the lack of cytological data, our preliminary observations suggest SEM and TEM studies should be essential for understanding the role of such structures. Of course histochemical and enzymological studies, as outlined by Gottsberger *et al.* (1998) should be conducted, but are feasible only on living or conveniently fixated flowers, thus entailing a laboratory work in field conditions.

The annonaceous gynoecium is remarkably diverse, but more attention should be paid to the detailed arrangement of carpels, which appears spiral from outside, but whorled in vasculature (as is also the case for the androecium). In the context of paracarpy, it appears that true syncarpy could potentially be induced from the central carpels by a rather simple experiment involving hormonal stimulation at a precise ontogenetical stage.

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## REFERENCES

- BRIECHLE-MÄCK M. H. 1994. — Beiträge zur Histogenese der Blüten und Früchte pseudosynkarper Annonaceen-Arten. *Deutsche Hochschulschriften* 1028: 1-133.
- CARLQUIST S. 1982. — The use of ethylenediamine for softening plant tissues. *Stain Technology* 57: 311-317. <https://doi.org/10.3109/10520298209066729>.
- CHATROU L. W., PIRIE M. D., ERKENS R. H. J., COUVREUR T. L. P., NEUBIG K. M., ABBOTT J. R., MOLS J. B., MAAS J. W., SAUNDERS

- R. M. K. & CHASE M. W. 2012. — A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. *Botanical Journal of the Linnean Society* 169: 5-40. <https://doi.org/10.1111/j.1095-8339.2012.01235.x>
- COUVREUR T. L. P., PIRIE M. D., CHATROU L. W., SAUNDERS R. M. K., SU Y. C. F., RICHARDSON J. E. & ERKENS R. H. J. 2011. — Early evolutionary history of the flowering plant family Annonaceae: steady diversification and boreotropical geodispersal. *Journal of Biogeography* 38: 664-680. <https://doi.org/10.1111/j.1365-2699.2010.02434.x>
- COUVREUR T. L. P., RICHARDSON J. E., SOSEF M. S. M., ERKENS R. H. J. & CHATROU L. W. 2008. — Evolution of syncarpy and other morphological characters in African Annonaceae: A posterior mapping approach. *Molecular Phylogenetics and Evolution* 47: 302-318. <https://doi.org/10.1016/j.ympev.2008.01.018>
- DEROIN T. 1987. — Anatomie florale de *Meiocarpidium* Engler & Diels (Annonaceae-Unoneae). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4e série, 9, sect. B, *Adansonia* 1: 81-93.
- DEROIN T. 1988a. — *Aspects anatomiques et biologiques de la fleur des Annonacées*. Unpublished thesis n°590, Université Paris 11, Orsay, France, 263 p.
- DEROIN T. 1988b. — Biologie florale d'une Annonacée introduite en Côte d'Ivoire: *Cananga odorata* (Lam.) Hook.f. & Thoms. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4e série, 10, sect. B, *Adansonia* 4: 377-393.
- DEROIN T. 1989. — Définition et signification phylogénique des systèmes corticaux floraux: l'exemple des Annonacées. *Comptes Rendus de l'Académie des Sciences*, Paris, t. 308, Série III: 71-75. <http://gallica.bnf.fr/ark:/12148/bpt6k62969160/f85.item>
- DEROIN T. 1991. — La répartition des modèles de plateaux stigmatiques et l'évolution des Annonacées. *Comptes Rendus de l'Académie des Sciences*, Paris, t. 312, Série III: 561-566. <http://gallica.bnf.fr/ark:/12148/bpt6k5866326q/f563.item>
- DEROIN T. 1997. — Confirmation and origin of the paracarpy in Annonaceae. *Candollea* 52: 45-58.
- DEROIN T. 1999. — Functional impact of the vascular architecture of flower in Annonaceae and Magnoliaceae, and its bearing on the interpretation of the magnoliaceous gynoeceum. *Systematics and Geography of Plants* 68: 213-224. <https://doi.org/10.2307/3668602>
- DEROIN T. 2010. — Floral anatomy of *Magnolia decudua* (Q.Y.Zheng) V.S.Kumar (Magnoliaceae): recognition of a partial pentamery. *Adansonia*, sér. 3, 32 (1): 39-55. <https://doi.org/10.5252/a2010n1a3>
- ENDRESS P. K. 1982. — Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive Angiosperms. *Taxon* 31: 48-52. <https://doi.org/10.2307/1220588>
- ENDRESS P. K. & ARMSTRONG J. E. 2011. — Floral development and floral phyllotaxis in *Anaxagorea* (Annonaceae). *Annals of Botany* 108: 835-845. <https://doi.org/10.1093/aob/mcr201>
- FRIES R. E. 1959. — Annonaceae, in ENGLER A. & PRANTL K. (eds), *Die Natürlichen Pflanzenfamilien*, ed. 2, 17a II. Duncker & Humblot, Berlin: 1-171.
- GENTRY A. 1993. — Diversity and floristic composition of lowland tropical forest in Africa and South America, in P. (ed.), *Biological Relationships between Africa and South America*. Yale University Press, New Haven, Connecticut: 500-547. [https://doi.org/10.1016/0169-5347\(94\)90166-X](https://doi.org/10.1016/0169-5347(94)90166-X)
- GERLACH D. 1984. — *Botanische Mikrotechnik*. Ed. 3. Thieme, Stuttgart, 393 p.
- GOTTSBERGER G., WEBBER A. C. & HILDENBRAND M. 1998. — Nutritious tissues in flowers of Annonaceae. *Annonaceae Newsletter* 12: 25-26.
- HEUSDEN E. C. H. VAN 1992. — Flowers of Annonaceae: morphology, classification, and evolution. *Blumea*, Suppl. 7: 1-218.
- JUSSIEU A.-L. DE 1789. — *Genera plantarum*. Paris: Herissant. <https://doi.org/10.5962/bhl.title.284>
- KESSLER P. J. A. 1993. — Annonaceae, in KUBITZKI K., ROHWER J. G. & BITTRICH V. (eds), *The Families and Genera of Vascular Plants*, Vol. 2. Magnoliid, hamamelid and caryophyllid families. Springer Verlag, Berlin, X: 93-129. <https://doi.org/10.1007/978-3-662-02899-5>
- LE THOMAS A. 1969. — Annonaceae, in AUBRÉVILLE A. (ed.), *Flore du Gabon*, vol. 16. Muséum national d'Histoire naturelle, Paris, 371 p.
- LE THOMAS A. 1980. — Ultrastructural characters of the pollen grains of African Annonaceae and their signification for the phylogeny of primitive angiosperms. First part. *Pollen & Spores* 22: 267-342.
- LE THOMAS A. 1981. — Ultrastructural characters of the pollen grains of African Annonaceae and their signification for the phylogeny of primitive angiosperms. Second part. *Pollen & Spores* 23: 5-36.
- PELLEGRIN F. 1920. — *Plantae Letestuanæ novæ* ou Plantes nouvelles récoltées par M. Le Testu de 1907 à 1919 dans le Mayombe congolais. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 1ère série, 26 (7): 654-659.
- PELLEGRIN F. 1924. — *Pseudartabotrys*, in La flore du Mayombe d'après les récoltes de M. Georges Le Testu. *Mémoires de la Société linnéenne de Normandie*, 2e série, 26: 15-16, inset pl. 5. <http://gallica.bnf.fr/ark:/12148/bpt6k9618264n/f75.item>
- PUNYASENA S. W., ESHEL G. & MCELWAIN J. C. 2008. — The influence of climate on the spatial patterning of Neotropical plant families. *Journal of Biogeography* 35: 117-130. <https://doi.org/10.1111/j.1365-2699.2007.01773.x>
- RAINER H. & CHATROU L. W. (eds) 2017. — AnnonBase: Annonaceae GSD (version Jan 2014), in ROSKOV Y., ABUCAY L., ORRELL T., NICOLSON D., BAILLY N., KIRK P. M., BOURGOIN T., DEWALT R. E., DECOCK W., DE WEVER A., NIEUKERKEN E. VAN, ZARUCCHI J., PENEV L. (eds), *Species 2000 & ITIS Catalogue of Life*, 29th September 2017. Digital resource at <http://www.catalogueoflife.org/col>. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-8858.
- SILBERBAUER-GOTTSBERGER I., GOTTSBERGER G. & WEBBER A. C. 2003. — Morphological and functional flower characteristics of New and Old World Annonaceae with respect to their mode of pollination. *Taxon* 52: 701-718. <https://doi.org/10.2307/3647345>
- TCHOUTO M. G. P., DE BOER W. E., DE WILDE J. J. F. E. & VAN DER MAESEN L. J. G. 2006. — Diversity Patterns in the Flora of the Campo-Ma'an Rain Forest, Cameroon: Do Tree Species Tell it All? *Biodiversity and Conservation* 15: 1353-1374. <https://doi.org/10.1007/s10531-005-5394-9>
- XUE B., SHAO Y.-Y., SAUNDERS R. M. K. & TAN Y.-H. 2017. — *Alphonsea glandulosa* (Annonaceae), a New Species from Yunnan, China. *PLoS ONE* 12(2): e0170107. <https://doi.org/10.1371/journal.pone.0170107>

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