

The genus complex *Danais-Schismatoclada-Payera* (*Rubiaceae*). Character states, generic delimitation and taxonomic position

R. BUCHNER & C. PUFF

Summary : Investigations of various character states clearly prove that the Madagascar-centred genera *Danais*, *Schismatoclada* and *Payera* (incl. *Coursiana*) are very closely allied. The genera had previously been associated with different tribes, namely the *Hedyotideae* (*Rubiaceae* subfam. *Rubioideae*) and the *Cinchoneae* (subfam. *Cinchonoideae*). Individual character states are described and discussed, and characteristics that can be used to distinguish the genera are given. Agreements and overlaps in certain features, that sometimes make it difficult to keep genera apart, are thought to be an expression of their close alliance rather than the result of convergent evolution. An analysis of the character states suggests that the genera in question can neither be clearly and objectively assigned to subfam. *Rubioideae* (tribe *Hedyotideae*) nor placed in subfam. *Cinchonoideae* because the genus complex contains features which, in part, are typical for one and, in part, characteristic for the other subfamily. The genera seem to provide further evidence for the view that the delimitation of the two subfamilies is not entirely clear-cut, and that there might be a systematic "grey zone" between the two subfamilies. Although there is some justification in tentatively creating a new tribe for the genera (without assigning it to any of the subfamilies), it is considered more reasonable to refrain from doing so and rather wait until more detailed, comparative data become available. — A survey of the taxa is appended; it includes several new combinations and the description of two new species of *Payera*.

Résumé : L'étude de plusieurs états de caractères montre clairement que les genres de la région malgache *Danais*, *Schismatoclada* et *Payera* (incl. *Coursiana*) sont très voisins. Ces genres ont été antérieurement rangés dans différentes tribus, à savoir les *Hedyotideae* (*Rubiaceae* subfam. *Rubioideae*) et les *Cinchoneae* (subfam. *Cinchonoideae*). Des états de caractères individuels sont décrits et discutés, et des caractéristiques pouvant être utilisées pour distinguer les genres sont données. Les concordances et les chevauchements pour certaines particularités, qui quelquefois rendent difficiles la séparation des genres, sont considérés comme l'expression de leur proche parenté plutôt que le résultat d'une évolution convergente. L'analyse des états de caractères suggère que les genres en question ne peuvent, ni être clairement et objectivement attribués à la sous-famille des *Rubioideae* (tribu *Hedyotideae*), ni placés dans la sous-famille des *Cinchonoideae*, parce que le complexe générique contient des particularités qui, en partie, sont typiques pour l'une et, en partie, caractéristiques pour l'autre sous-famille. On trouve dans ces genres des preuves complémentaires confirmant l'opinion que la délimitation des deux sous-familles n'est pas tout à fait nette, et qu'il doit exister une « zone d'ombre » systématique entre elles. Bien qu'il soit légitime de tenter de créer une nouvelle tribu pour ces genres (sans la rattacher à aucune des sous-familles), il semble plus raisonnable de s'abstenir d'agir ainsi et plutôt d'attendre que des données comparatives plus détaillées deviennent disponibles. — Un exposé sommaire des taxa est présenté en annexe; il inclut plusieurs nouvelles combinaisons et la description de deux nouvelles espèces de *Payera*.

Ralf Buchner & Christian Puff, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria.

I. INTRODUCTION

The initial aim of the present study was to investigate a broad spectrum of character states of *Danais* species in order to obtain detailed data for an evaluation of the genus' correct placement. Up to now, there has been much debate about the taxonomic (tribal and subfamilial) position of *Danais* (see Taxonomic History, below, for details).

During these investigations it, however, soon became obvious that the generic delimitation of *Danais* is not as clear-cut as thought previously. It was noted that there are sometimes considerable problems in separating *Danais* and the Malagasy endemic *Schismatoclada* which, like the former, is of uncertain tribal position. Moreover, it surfaced that the monotypic *Coursiana* (tribe *Cinchoneae*, subtribe *Cinchoninae*), yet another Malagasy endemic, is in turn very close to the pair *Danais-Schismatoclada*. Finally, a by-chance discovery brought to light a previously never thought-of obvious relationship between the Malagasy endemic *Payera* (tribe *Hedyotideae*, subfam. *Rubioideae*) and the three before-mentioned genera.

Consequently, the aims of the study changed : Next to *Danais*, all other genera of this obviously allied complex had to be dealt with. The problems regarding their generic delimitation had to be tackled, and the question of their taxonomic status (i.e., tribal and subfamilial position) needed to be resolved.

II. MATERIAL AND METHODS

Material of *Danais*, *Schismatoclada*, *Coursiana* and *Payera* from the following herbaria was studied : BM, BR, K, M, MO, P, UPS, W and WU (abbreviations according to "Index Herbariorum", HOLMGREN et al., 1990). A total of nearly 900 sheets was seen; it is important to note that not all material of *Schismatoclada* in herbarium P was available for study.

Moreover, samples preserved in FPA or 70% ethanol were available of several taxa for detailed morphological and anatomical investigations.

Illustrations were prepared from the following vouchers (deposited at WU, unless an other herbarium abbreviation is given; from Madagascar unless stated otherwise; * = preserved material) :

Danais aurantiaca Homolle : Gentry 11271 (MO) (Fig. 10, D). — *D. coronata* (Pers.) Steud. : Decary 10767 (P) (Fig. 11, E-G). — *D. fragrans* (Lam.) Pers. : Mauritius : Guého s.n. (WU)* (Fig. 1, A-C; 5, E-F; 6; 7, A-D, F-K; 8, A; 15, A-C); Madagascar : Benoist 1217 (P) (Fig. 7, E; 12, A-D), Jardin Botanique Tana 3858 (P) (Fig. 15, D-F), Lowry & Randrianasolo 4422 (MO) (Fig. 13, A-D), Schatz 1389 (MO) (Fig. 4, A from colour slide Schatz). — *D. humblotii* Homolle : Puff et al. 850824-1/9 (WU)* (Fig. 2, A-B; 8, C-D). — *D. ligustrifolia* Baker : Cours 4451 (P) (Fig. 17, A-B), Decary 14191 (P) (Fig. 10, C; 11, A-D; 12, G). — *D. microcarpa* Baker : Puff et al. 850824-1/7 (WU)* (Fig. 1, H). — *D. pubescens* Baker : Baron 1375 (P) (Fig. 12, E), Puff et al. 850824-1/8 (WU)* (Fig. 1, G; 12, F). — *D. rhamnifolia* Baker : Decary 5055 (P) (Fig. 11, A), Perrier de la Bâthie 12593 (P) (Fig. 15, J; 17, C-D). — *D. volubilis* Baker : Bosser 6616 (P) (Fig. 10, A-B), Jardin Botanique Tana 3861 (P) (Fig. 15, H-I), Puff et al. 850808-1/1 (WU)* (Fig. 1, D-F; 5, A-D, G-H; 8, B; 13, E; 15, G; Fig. 4, B-C from colour slides Puff mad-1781 and mad-1782).

Payera bakeriana (Homolle) Buchner & Puff : SF 22640 (P) (Fig. 14, B-C). — *P. coriacea* (Humbert) Buchner & Puff : Humbert 22762 (P) (Fig. 16, C), Humbert & Cours 23823 (P) (Fig. 16, A-B, D), Miller &

Lowry 4151 (MO) (Fig. 2, E-F). — *P. decaryi* (Homolle) Buchner & Puff : Decary 10839 (P) (Fig. 14, E-F), Puff 800808-1/3 (WU)* (Fig. 2, D; 9; Fig. 4, D from colour slide Puff mad-0491), Schatz & Nicoll 1236 (MO) (Fig. 10, I-K). — *P. glabrifolia* Leroy ex Buchner & Puff : Cours 4930 (P) (Fig. 4, E). — *P. homolleana* (Cavaco) Buchner & Puff : Cours 2756 (P) (Fig. 14, D).

Schismatoclada psychotrioides Baker : Gentry 11856 (MO) (Fig. 2, C), Schatz et al. 1376 (MO) (Fig. 10, E-H; 14, A). — *S. viburnoides* Baker : Croat 28889 (MO) (Fig. 16, G), Miller & Lowry 4121 (MO) (Fig. 16, E-F).

Methods used agree with those described in PUFF et al. (1993) except for the following supplements and additions :

For SEM investigations, microtome and hand sections, samples from herbarium material were first reconstituted in a mixture (6 : 1) of 10 % aqueous bis (2-ethylhexyl) sulfosuccinate sodium salt and 98 % acetone for ca. 6 to 24 hours (modified from PETERSON et al., 1978).

For TEM studies of pollen and seeds, samples from herbarium specimens were embedded in Spurr's mixture (SPURR, 1969) and then ultra-thin sectioned (90 nm). Sections were contrasted with uranylacetate and lead citrate. The polysaccharide test was carried out manually according to THIÉRY (1967) and WEBER (1989), respectively.

For LM investigations of pollen, grains were transferred to a mixture of methyl green and glycerine gelatine according to WODEHOUSE (1935); measurements were made on pollen grains so prepared. For the determination of pollen nuclear numbers, pollen grains preserved in FPA were stained with acetocarmine.

Notes on names used in the present article : In order to avoid confusion, only accepted names are used in the chapters following the "Taxonomic History" section (*Danais* : see revision of the genus, PUFF & BUCHNER, in press; *Schismatoclada* and *Payera* : see Appendix). Only if absolutely necessary, the original generic association of a specific name will be given in square brackets, e.g. "*Payera* [*Danais*] *bakeriana*" for *P. bakeriana* (Homolle) Buchner & Puff (syn. *Danais bakeriana* Homolle). *Coursiana* will be shown to be congeneric with *Payera* (see Appendix); to stress the original generic association of its only species, "*Payera* [*Coursiana*] *homolleana*" will occasionally be used.

III. TAXONOMIC HISTORY (Table 1)

Following the descriptions of *Danais* species in the nineteenth century, M^{me} HOMOLLE (1936) published numerous new Malagasy species of the genus, mostly based on material of BARON and of French collectors such as PERRIER DE LA BÂTHIE, DECARY, or HUMBERT. New taxa were added by CAVACO (1965, 1966 and 1968b). In one of his publications (CAVACO, 1966), he included a key to the Malagasy and Comoro Island species he recognized. Unfortunately, this publication did not give any details on the species and, moreover, also included some new names which were not formally validated.

The same authors also dealt with *Schismatoclada*, a genus endemic to the East Malagasy region (HOMOLLE, 1939; CAVACO, 1964, 1967, 1968a). Both of them accepted the genus as it was and did not at all discuss the relationships to *Danais*.

In the most recent overall treatment of the *Rubiaceae* (ROBBRECHT, 1988), *Danais* and *Schismatoclada* are listed amongst those genera whose taxonomic position is uncertain. In the past, the two genera have on the one hand been associated with the tribe *Cinchoneae* (subfam. *Cinchonoideae*) and, on the other, been referred to tribe *Hedyotideae* (subfam. *Rubioideae*) (see Table 1). Dealing with the circumscription of the *Cinchoneae*, ANDERSSON & PERSSON (1991)

provisionally transferred both genera to the *Hedyotideae*. The arguments that have, over the years, been brought forward in favour of or against a particular placement of either of the two genera will be discussed in the final chapter.

TABLE 1 : Tribal position of **Danais**, **Schismatoclada**, **Coursiana** and **Payera** (year of establishment in brackets) according to different authors. — Abbreviation of tribes : Cin : Cinchoneae; Hed : Hedyotideae; Cin/Hed : intermediate; Cin-C : Cinchoneae-Cinchoninae; — : not dealt with.

Author	<i>Danais</i> (1799)	<i>Schismatoclada</i> (1883)	<i>Coursiana</i> (1942)	<i>Payera</i> (1878)
ENDLICHER (1838), HOOKER (1873), DRAKE (1898b), BREMEKAMP (1948)	Cin	—	—	—
BAILLON (1880)	Cin	—	—	“Genipeae” ¹
BAKER (1883), HOMOLLE (1939)	—	Cin	—	—
SCHUMANN (1891)	Cin	Cin	—	“Oldenlandieae” ²
HOMOLLE (1942)	—	—	Cin	—
BOITEAU (1941)	Cin	Cin	—	—
BREMEKAMP (1952, 1966)	Hed	[Cin] ³	Hed	—
VERDCOURT (1958)	Hed	Hed	Hed	—
CAVACO (1964, 1966, 1968a, 1968b)	Cin	Cin	Cin	—
ROBBRECHT (1988)	Cin/Hed	Cin/Hed	Cin-C	Hed
ANDERSSON & PERSSON (1991)	Hed ⁴	Hed ⁴	Hed ⁴	—

1. “nr. *Myrioneuron*” (the latter is now placed in tribe Isertieae; cf. ROBBRECHT, 1988).

2. Is ± Hed; see text.

3. Not specifically mentioned; infers that either the inclusion in Cin was not doubted or that the genus was unknown to him; see text.

4. Provisional transfer suggested.

The genus *Coursiana* was established in 1942 by M^{me} HOMOLLE, although she never specifically mentioned a type species. This was eventually rectified by CAVACO (1968a) by describing *Coursiana homolleana*, the only species ever described in this East Malagasy genus. M^{me} HOMOLLE (1942) had made absolutely no reference to *Danais* and *Schismatoclada* when she described *Coursiana*, although she had dealt with the two genera in 1936 and 1939, respectively (see above). It is difficult to understand that she should not have been aware of the close association between these three genera. CAVACO (1968a) did not discuss the relationships of *Coursiana* either and uncritically accepted M^{me} HOMOLLE’s suggestion of placing the genus in the tribe *Cinchoneae* (subtribe *Cinchoninae*).

The tribal position of *Coursiana* was also accepted by ROBBRECHT (1988), although both BREMEKAMP (1952, 1966) and VERDCOURT (1958) had suggested a transfer to the *Hedyotideae*. ANDERSSON & PERSSON (1991) also favoured a position in the latter tribe.

Notes on and attached to herbarium sheets in P indicate that Prof. J.-F. LEROY, former director of the Paris herbarium, dealt with *Danais*, *Schismatoclada* and *Coursiana* in 1975. It was he who discovered that the rather ill-known monotypic Malagasy endemic genus *Payera* is

apparently closely allied to the above mentioned complex of genera. It can be reconstructed from his notes that he initially intended to transfer *Coursiana* and species of *Schismatoclada* to *Payera*. He later changed his mind and apparently thought that the complex of four genera is best combined into one genus, i.e., *Danais* VENTENAT (1799) [= *Payera* BAILLON (1878), = *Schismatoclada* BAKER (1883), = *Coursiana* HOMOLLE (1942)]. Prof. LEROY, however, never published his findings.

While Prof. LEROY's concept of "*Danais* s.l." is not accepted (see below), his discovery of the genus *Payera* being part of this alliance is certainly a highly valuable contribution which, most likely, would have remained unknown otherwise.

The genus *Payera*, originally placed in the "*Genipeae*" (BAILLON, 1880), was considered to be a member of the *Oldenlandieae* (which to some extent correspond to the *Hedyotideae* as circumscribed today) by SCHUMANN (1891). The ill-known genus was not specifically dealt with by other authors, and ROBBRECHT (1988) accepted its position in the *Hedyotideae*.

IV. RESULTS : THE CHARACTER STATES

VEGETATIVE CHARACTERISTICS

1. GROWTH FORM, STEMS

Danais : The entire genus is comprised of woody lianas or climbing shrubs, some of which may reach considerable dimensions. *D. magna* and *D. ligustrifolia*, for example, are reported to produce shoots which reach ca. 25 m into the canopy of rain forest trees. Others are less extensive; their shoots apparently do not become longer than a few meters.

The lianas of *Danais* appear to be several - to many - stemmed throughout. According to field observations by one of us (C. P.), stems are normally rather much-branched above. Ultimate branches do not twine.

Descriptions of "climbing shrubs" indicate that the basal parts of plants indeed have a fundamentally shrubby structure (i.e. several - to many - stemmed), from which markedly elongated and climbing axes arise.

If the main shoots are not yet so long that they can climb up on the surrounding higher vegetation (younger individuals!), plants may resemble "typical" shrubs. Moreover, plants growing in surroundings which lack higher vegetation, develop shoots which bend downwards to the ground and even \pm creeping shoots (this, has, for example, been noted for *D. coronata*, which typically grows in forest edge vegetation). Descriptions on herbarium labels of *Danais* species as shrubs probably refer to such situations and are, therefore, somewhat misleading in that they do not reflect the true situation.

In *Danais*, younger shoots are either glabrous or somewhat hairy. If present, hairs — uniseriate and several-celled throughout — are normally rather short; only in a few species (e.g. *D. vestita* and *D. hispida*), relatively long hairs and a dense stem indumentum are present. Older stems tend to become glabrescent.

The lianaceous habit separates *Danais* from *Schismatoclada* and *Payera*. The latter are normally described as either shrubs or small trees up to a few meters tall.

In *Schismatoclada*, shoots are typically glabrous, while in *Payera* they are often densely hairy (at least the youngest parts).

In both, the ultimate parts of twigs often show conspicuous sympodial-dichasial branching (because of the invariably terminal position of the inflorescences).

2. LEAVES AND STIPULES

a. STIPULES

In all genera dealt with, the interpetiolar stipules are variable in size and shape.

Danais typically has triangular to \pm deltoid or \pm rounded stipules (up to ca. 8 mm, rarely to 15 mm long). There are few exceptions, e.g. *D. andribensis* with consistently bifid stipules and *D. vestita* with stipules which bear several to many fimbriate appendages; *D. brickavillensis* has rounded stipules with lacinate margins.

In both *Schismatoclada* and *Payera*, the stipules are either entire or variously divided. Quite frequently, the stipules of *Schismatoclada* are \pm connate at the base; they tend to be small (to ca. 3 mm long) and often entire (e.g. *S. viburnoides*, Fig. 4, G) but there are also species with rather large, pluri- to multifimbriate stipules (e.g. *S. longistipula*, cf. CAVACO, 1967 : Fig. 1, 1-2). In *Payera*, a very clear trend towards large, conspicuous, almost leaf-like stipules is noticeable (e.g. *P. glabrifolia*, Fig. 4, E). *P. decaryi* has elliptic to lanceolate-elliptic stipules which are to ca. 45 mm long. Not uncommonly the stipule margins are lacinate or bear fimbriate appendages. Within the genus there are, however, also small-stipuled species (e.g. *P. madagascariensis*, stipules only a few mm long).

In many taxa of all three genera, the stipules are \pm persistent and frequently recognizable as dried, somewhat hardened structures on old shoot portions. Large-stipuled *Payera* species appear to be an exception (stipules often disappear together with the leaf-blades).

Colleters are normally present on the inside and on the margins of the stipules. The conical colleters correspond to the standard type which is known to occur in many other taxa of the *Rubiaceae* (cf. ROBBRECHT, 1988).

b. LEAF MORPHOLOGY

In all genera dealt with, decussate leaf arrangement predominates. In a few taxa of *Danais*, however, true whorls of three and/or four do occur regularly (e.g. *D. coronata*, *D. verticillata* and *D. volubilis*; within *D. cernua*, both decussate and ternate leaf arrangement was observed). Also *Schismatoclada marojejyensis* has leaves arranged in whorls of three.

The leaves are typically petiolate. In *Danais* and *Payera*, petiole lengths range from ca. 1.5 to ca. 35 mm. In some taxa, e.g. morphs of *D. pubescens* or *P. coriacea*, petioles are short (ca. 1.5-3 mm); *D. verticillata* has sessile leaves. The longest petioles, to ca. 30-35 mm long, occur in *D. magna* and *D. decaryi*. In *Schismatoclada*, petioles tend to be very short to short (i.e., 1 to 10 mm); due to long-cuneate leaf-blade bases leaves may even be sessile (e.g. *S. humbertiana*).

Sizes and shapes of the leaf-blades vary considerably within the genera (and sometimes also within individual species).

Common are size ranges from ca. 20 to 120 mm. Exceptions are *P. decaryi*, with leaf-blades to over 300 mm long, morphs of *D. pubescens* (“*D. nummularifolia*-forms”, see PUFF & BUCHNER, in press) with blades less than 20 mm long, and *S. marojejyensis*. The latter is a microphyllous species (blades hardly more than 10 mm long) occurring in “ericoid” high mountain vegetation.

Obovate, ovate, elliptic, elliptic-lanceolate to linear-lanceolate leaf-blade shapes are frequent. Apices are often acuminate (very conspicuous, long-acuminate in, e.g., *D. tsaratananensis*), shortly pointed or \pm rounded; emarginate apices (e.g. in morphs of *D. pubescens*) are rather rare. The bases of the blades are most commonly (\pm) cuneate.

Most (or all?) taxa of all three genera appear to have evergreen leaves. While the leaves of all *Schismatoclada* species seem to be invariably rather thick and leathery, both in *Danais* and *Payera*, two groups of taxa can be distinguished. One has thick, leathery (distinctly coriaceous) leaves (e.g. *D. fragrans*, *D. volubilis*, *D. coronata*; *P. coriacea*). The other has leaves which tend to be relatively thin (less distinctly coriaceous; e.g. *D. microcarpa*, *D. ligustrifolia*; *P. decaryi*). The rather thinnish leaves of some taxa of *Payera* might be short-lived and deciduous, but this needs confirmation in the field.

Especially for taxa of *Payera* it seems to be characteristic that leaves are crowded on the very terminal parts of long shoots (e.g. *P. decaryi*, Fig. 4, D).

In *Danais* and *Payera*, there are both glabrous and hairy taxa; in contrast, the leaves of *Schismatoclada* tend to lack an indumentum. In hairy taxa, the indumentum, although invariably comprised of uniseriate, pluricellular hairs, varies in extent and length and shape of the hairs. The leaf blades are either hairy above and below (e.g. *P. homolleana*), or only on one of the surfaces, or only on the midrib below (e.g. *P. beondrokensis*). Hairs may be short or long and \pm curled and dense (woolly to velvety indumentum, e.g. *D. vestita*, *D. pubescens*).

Rather frequently, the indumentum varies within taxa, i.e., in essentially “hairy” taxa, there may be morphs in which the indumentum is only sparsely developed or almost lacking (e.g. in *D. hispida* or *D. pubescens*).

The venation of the leaf blades is conspicuous in some taxa of *Danais* and *Payera*. Due to raised secondary and higher order veins, reticulate venation patterns may either be very prominent on the upper (e.g. *D. aurantiaca*) or on the lower blade surface (e.g. *P. homolleana*).

c. LEAF ANATOMY (Fig. 1-2; Table 2)

— Epidermis, incompletely multiple epidermis; hypodermis

In all three genera dealt with, the **lower epidermis** is always smaller-celled than the upper. Without exception, it was found to be one-layered and contains the stomata (leaves of all taxa are hypostomatic). The **stomatal apparatus** invariably is of the characteristic “rubiaceous type” (WILKINSON, 1979). The stomata are sometimes slightly raised (cf. Fig. 1, F; 2, F). Very markedly and conspicuously raised stomata, as depicted for *P. [Coursiana] homolleana* (HOMOLLE, 1942; Fig. 2), were not detected. Wax crystals were rather frequently noted in the area of the stomata and also elsewhere on the lower surface (e.g. *D. fragrans*, Fig. 1, B-C).

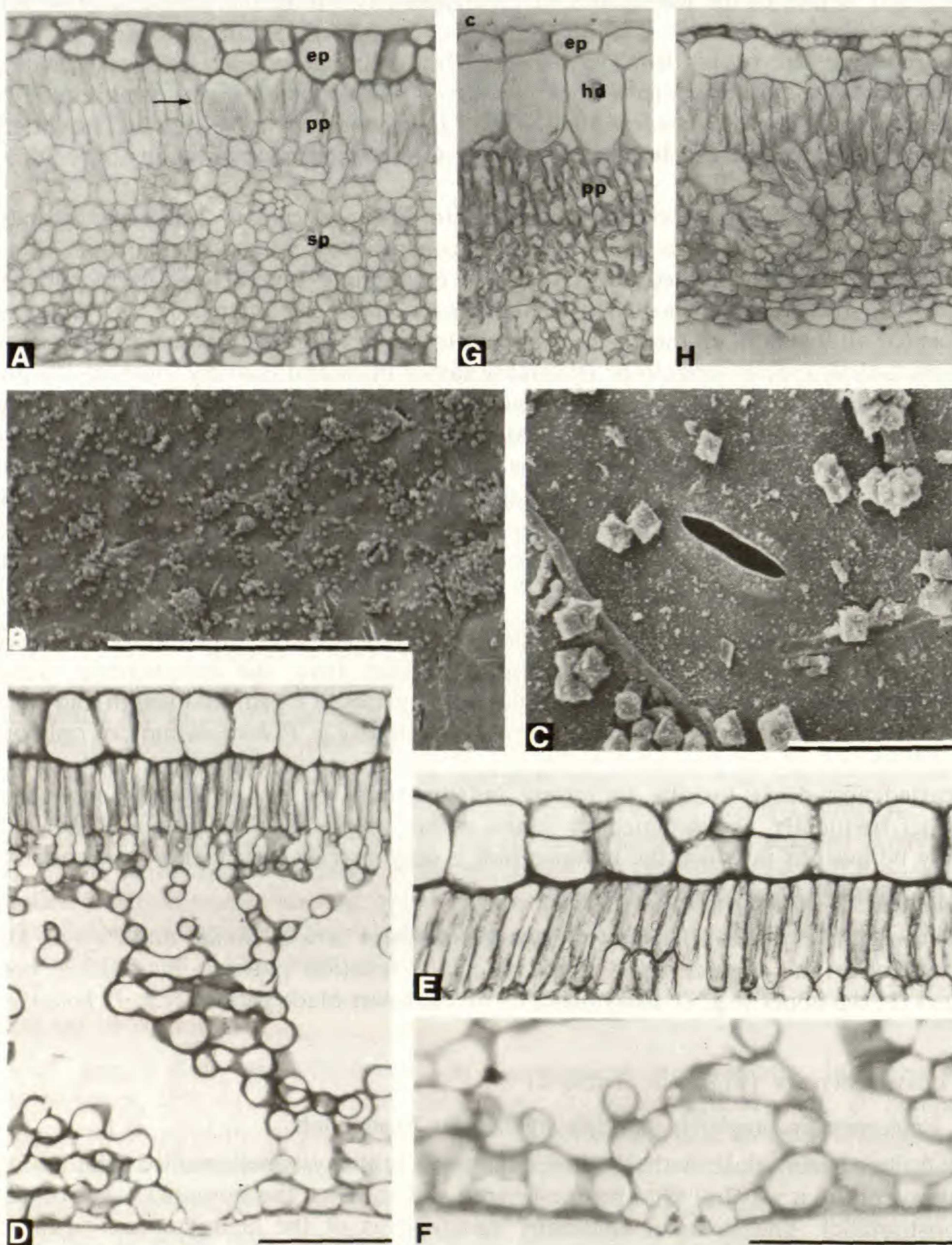


Fig. 1. — A, D-H, leaf sections of *Danais* species : A, *D. fragrans*; D-F, *D. volubilis*; E, detail showing incompletely multiple epidermis and palisade cells; F, detail of spongy mesophyll, lower epidermis and stoma; G-H, species with epi- and hypodermis; G, *D. pubescens*; H, *D. microcarpa*. — B-C, SEM-graphs of lower leaf surface of *D. fragrans* showing wax crystals and stoma (C). — ep, epidermis; hd, hypodermis; pp, palisade parenchyma; sp, spongy mesophyll. — Scale bars : 100 μm (A = D = G = H; B; E = F); 10 μm (C).

As regards the **upper epidermis**, the situation is heterogeneous. In *Schismatoclada* and all but one of investigated *Payera* species, there is a single layer of large cells (Fig. 2, C-D). In *Danais*, there are two groups of taxa. In one (taxa with relatively thin, although evergreen leaves, *D. microcarpa* and others, cf. Table 2), a “normal” single-layered upper epidermis is present, but below it there is a conspicuous, continuous **hypodermis** layer comprised of cells roughly three times as large as those of the epidermis (Fig. 1, G-H; 2, A-B). In the other group (taxa with thick, leathery leaves, *D. fragrans* and others, cf. Table 2), there is an “incompletely” (i.e., not continuously) several-(normally two-)layered epidermis (Fig. 1, A, D-E). As opposed to a true hypodermis (for information on the ontogeny of leaf blades and the origin of hypodermal layers see NAPP-ZINN, 1973), the multiple epidermis apparently comes about by the development of cross walls parallel to the upper-surface. This characteristic epidermis structure has, by the way, been illustrated correctly for *D. volubilis* by DUBARD & DOP (1925 : Fig. IV, 1, as “*Alleizettea bracteata*”).

The upper epidermis has a **cuticle** which, particularly in the coriaceous-leaved taxa, may be very thick and conspicuous. The cuticle of the lower epidermis generally is considerably thinner.

TABLE 2 : Selected leaf anatomical characters of **Danais**, **Schismatoclada** and **Payera**.
 — * = based on the investigation of preserved material (all others : herbarium material). — # several hypodermis layers; see text.

Rather small-celled upper epidermis, large-celled hypodermis below it	Large-celled, mostly incompletely multiple upper epidermis; hypodermis absent	“Normal” large-celled upper epidermis; hypodermis absent
<i>Danais aurantiaca</i> <i>D. cernua</i> <i>D. hispida</i> <i>D. humblotii</i> * (Fig. 2, A-B) <i>D. ligustrifolia</i> <i>D. magna</i> <i>D. microcarpa</i> * (Fig. 1, H) <i>D. nigra</i> <i>D. pubescens</i> * (Fig. 1, G) <i>D. rhamnifolia</i> <i>D. verticillata</i>	<i>Danais</i> : <i>D. andribensis</i> <i>D. coronata</i> <i>D. dauphinensis</i> <i>D. fragrans</i> * (Fig. 1, A) <i>D. terminalis</i> <i>D. tsaratananensis</i> <i>D. vestita</i> <i>D. volubilis</i> * (Fig. 1, D-F)	<i>Schismatoclada</i> : <i>S. humbertiana</i> <i>S. marojejyensis</i> <i>S. psychotrioides</i> (Fig. 2, C)
<i>Payera coriacea</i> * (Fig. 2, E-F)#		<i>Payera</i> : <i>P. decaryi</i> (Fig. 2, D) <i>P. [Coursiana] homolleana</i> *

— Mesophyll

In all three genera, the palisade parenchyma is always much less extensive than the spongy mesophyll. The former is normally made up of two to three layers of elongated, cylindrical (e.g. *D. volubilis*, Fig. 1, D-E) to \pm isodiametric (e.g. *P. decaryi*, Fig. 2, D), rather tightly packed cells. Numerous idioblasts filled with raphides tend to present particularly in the

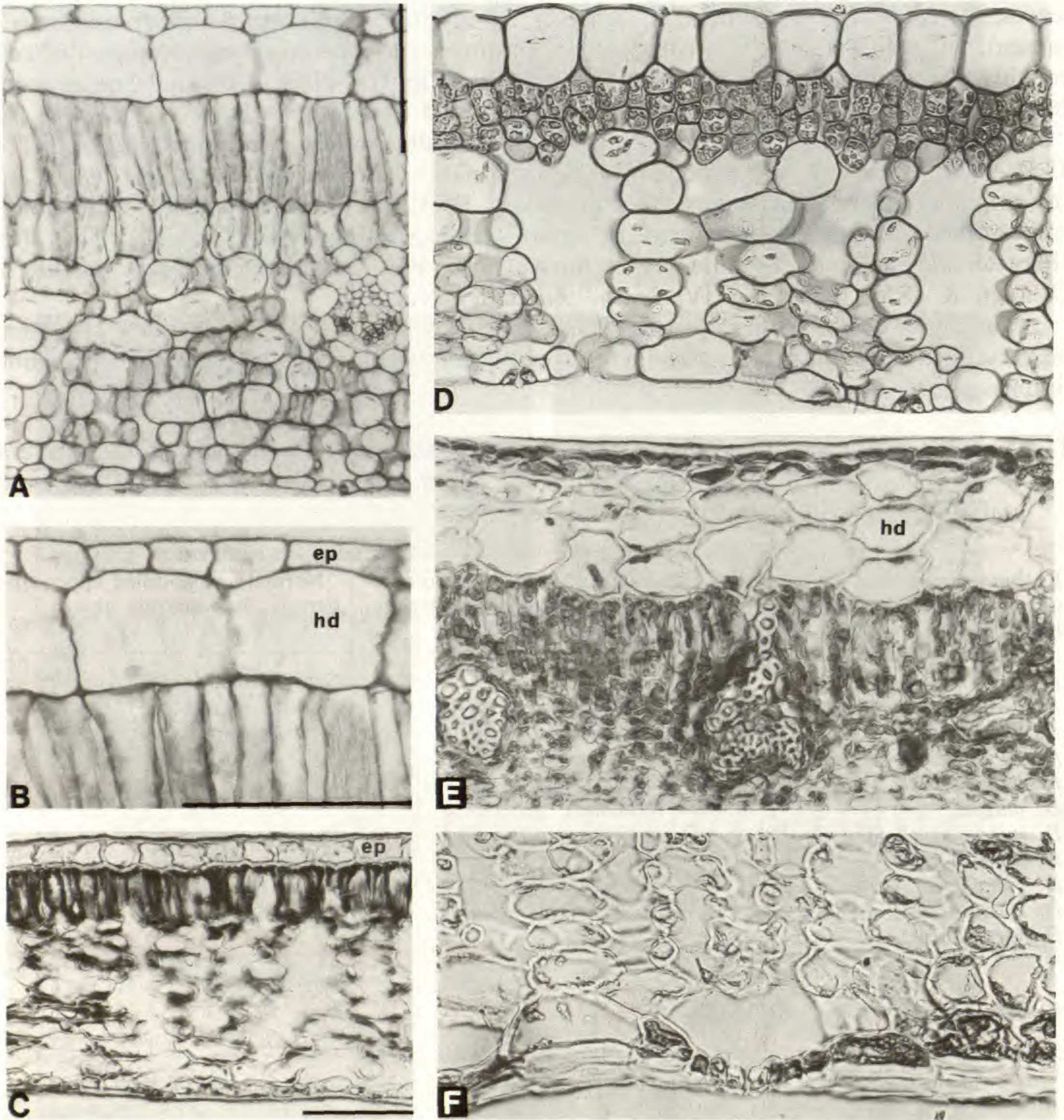


Fig. 2. — Leaf sections : A-B, *Danais humblotii*; B, detail showing epi- and hypodermis. — C, *Schismatoclada psychotrioides*. — D, *Payera decaryi*. — E-F, *P. coriacea*; E, note epidermis and several hypodermis layers and vascular bundles with sclerenchymatic bundle sheaths; F, part of spongy mesophyll, lower epidermis and stoma. — C, E-F, from reconstituted herbarium material. — Abbreviations as in Fig. 1. — Scale bars : 100 μ m (A ; B = D = F ; C = E).

palisade layer (Fig. 1, *A*). The spongy mesophyll is either rather compact (especially in *Danais*, e.g. *D. fragrans*, *D. microcarpa*, *D. pubescens*, Fig. 1, *A*, *G-H*) or very loose, containing large intercellular spaces (*Danais*, *Schismatoclada* and *Payera* spp., e.g. *D. volubilis*, *S. psychotrioides*, *P. decaryi*; Fig. 1, *F*; 2, *C-D*).

— Veins

Major veins (i.e., mid-rib and primary lateral veins) normally interrupt the mesophyll. A massive bundle sheath is either found above and below the actual bundle, or entirely surrounds it. The sheath is either sclerenchymatic in the immediate vicinity of the bundle and parenchymatic towards to upper and lower epidermis (e.g. *D. fragrans*) or sclerenchymatic and thick in its entirety (e.g. *D. aurantiaca* or *P. coriacea*).

Smaller vascular bundles are normally embedded in the spongy mesophyll; their sheaths tend to be confined to one or a few layers of parenchymatic or sclerenchymatic cells which do not extend to the epidermis (e.g. *P. coriacea*, Fig. 2, *E*).

FERTILE REGION

3. INFLORESCENCES (Fig. 3-4)

The basic inflorescence structure of all genera dealt with here is in conformity with the “basic type of *Rubiaceae* inflorescence” as defined by WEBERLING (1977), i.e., a many-flowered thyrses or pleiothyrses (or thyrses-paniculate?) inflorescence with an end (terminal) flower.

With regard to the position of the inflorescence in relation to the main axis, the genera show differences: *Schismatoclada* and *Payera* invariably have terminal inflorescences (cf. Fig. 3, *F-K*; 4, *D-G*). In addition to the “main” terminal inflorescence, there may sometimes also be a few solitary or paired axillary inflorescences arising further below on the main axis, but strictly axillary inflorescences seem to be entirely lacking.

In *Danais*, in contrast, there are two groups of species, one with predominantly terminal inflorescences (e.g. *D. rhamnifolia*, Fig. 3, *E*, etc.), the other with predominantly axillary inflorescences (e.g. *D. cernua*, *D. coronata*, etc.; cf. Fig. 3, *A-D*; 4, *A-C*), whereby the latter are paired or — depending on the leaf arrangement — also whorled. The latter category represents proliferating inflorescences (*sensu* WEBERLING, 1977; Fig. 3, *A*), in which the main axes remain in vegetative state. Proliferation does, however, not appear to be strictly obligatory in these taxa; it was sometimes observed that (although normally rather small) terminal inflorescences may occasionally be produced in addition to the axillary inflorescences.

Axillary inflorescences invariably arise in the axils of foliage leaf-like bracts. Bracts in the ultimate inflorescence regions are usually small to minute. Only in extensive, terminal inflorescences, bracts in the very basal portions may still be \pm foliage-leaf like; further up they soon become considerably smaller.

It deserves mentioning that, especially in *Danais* spp., bracts in the distal inflorescence portions are often no longer strictly opposite but somewhat displaced (cf., for example, Fig. 3, *G-H*).

The following modifications of the presumably basic, extensive, many-flowered thyrse or thyrses-paniculate type occur (Fig. 3):

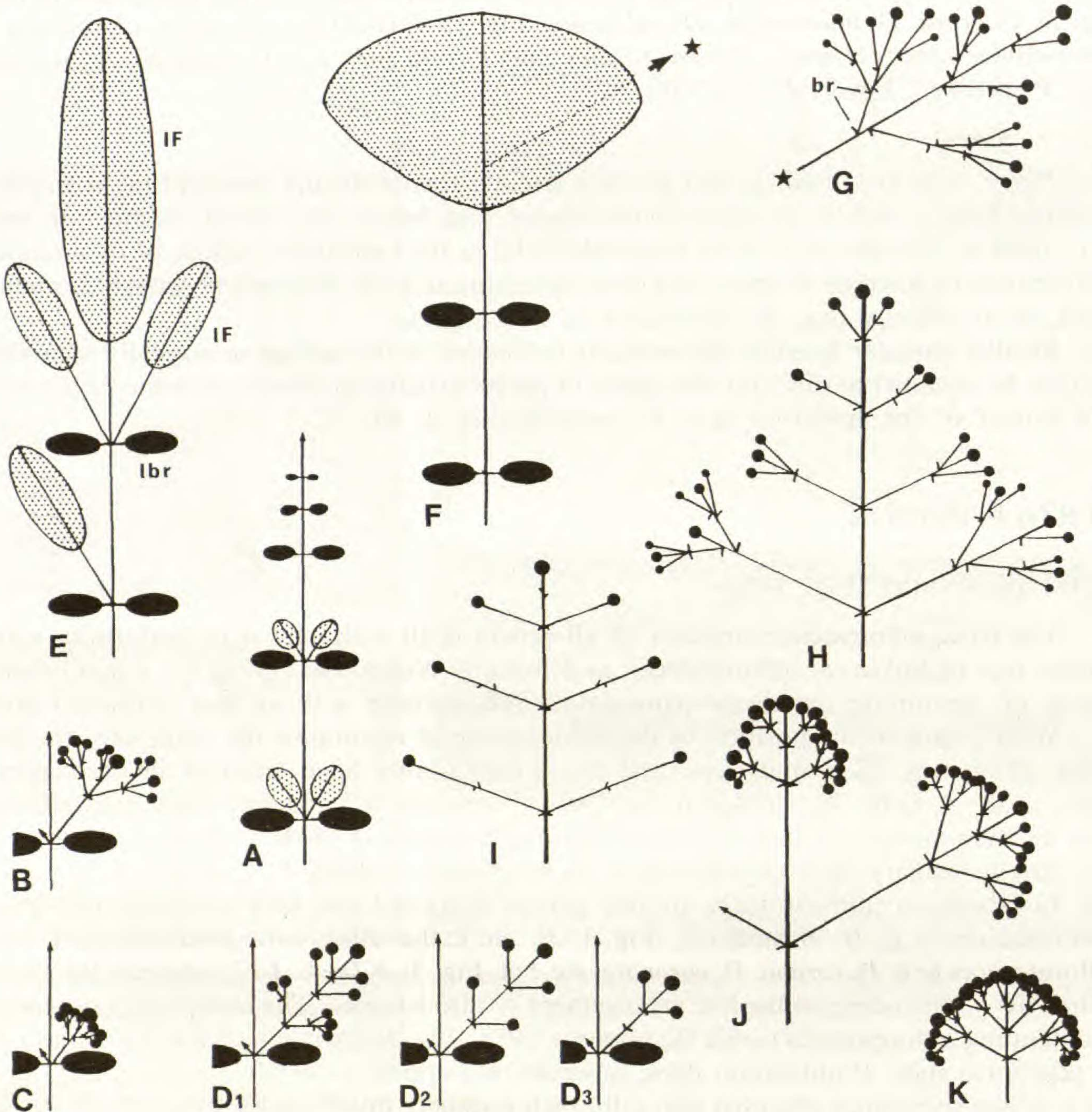


Fig. 3. — Inflorescences of *Danais*, *Schismatoclada* and *Payera* (schematic): A, E-F, diagrams of axillary and terminal inflorescence systems (IF, inflorescence; lbr, foliage leaf-like bract), all others stick diagrams of partial or entire inflorescences (br, small to minute bracts). — A-D, *Danais*, axillary inflorescences; A, diagram showing proliferating main axis; B, pedunculate axillary inflorescence (e.g. *D. hispida*); C, \pm sessile axillary inflorescence (e.g. *D. cernua*); D₁-D₂, *D. coronata*, increasingly reduced (i.e., fewer-flowered) axillary inflorescences. — E, terminal inflorescence and additional axillary inflorescences arising below (*Danais* spp., e.g. *D. rhamnifolia*). — F-K, terminal inflorescence found in all three genera. — G, partial inflorescence from F (e.g. *D. humblotii*, *Schismatoclada* spp.). — H-I, increasingly reduced (i.e., fewer-flowered) inflorescences (species pair *D. nigra* and *D. terminalis*). — J-K, increasing congested and \pm head-like inflorescences (especially *Schismatoclada* and *Payera* species). — Axes mostly not drawn to scale; in congested inflorescence types, internodes are shown longer than they actually are; black dots represent flowers, dot diameters indicate opening sequence (a terminal flower of a 3-flowered cyme is shown as a larger dot than the two lateral flowers). — Further explanations in the text.

1. *Increasing depauperation of a thyse*

In the extreme, the inflorescence is only very few-flowered, and partial inflorescences may not be more than one-flowered (i.e., consist of the terminal flower only); *Danais terminalis* (Fig. 3, *I*) is an example for this. In *Schismatoclada marojejensis*, the entire terminal inflorescence seems to have become one-flowered: only \pm sessile solitary flowers are present (cf. HUMBERT, 1955a: Fig. 10, 13, also reproduced in CAVACO, 1968a: Fig. 3, 10).

2. *Increasing congestion of partial or entire inflorescences* (due to the shortening of inflorescence axes, i.e., peduncles and pedicels)

In the case of taxa with very extensive terminal inflorescences, this results in the formation of head-like clusters in the ultimate inflorescence portions (e.g. *D. breviflora* or *P. decaryi*, Fig. 4, *D*; Fig. 3, *J*). Less extensive terminal inflorescences may become congested and head-like in their entirety (e.g. *P. glabrifolia*: Fig. 3, *K*; Fig. 4, *E*).

In *Danais* species with axillary inflorescences, shortening of all inflorescence axes results in the formation of sometimes rather dense flower clusters in the axils of foliage leaves (cf. Fig. 3, *C*); \pm stalked, head-like axillary flower clusters result if the basal internodes of an inflorescence remain largely unshortened (Fig. 3, *B*).

3. *Change in the branching of the ultimate elements of partial inflorescences*

The typical situation is "normal" sympodial-dichasial branching (three-flowered cymes; Fig. 3, *D*₃), but it is not too uncommon that partial inflorescences show a clear trend towards sympodial-monochasial branching, i.e. towards the formation of scorpioid cymes (cf. Fig. 3, *G*); this was noted in taxa of all genera dealt with.

4. FLOWERS

In all genera dealt with here, the flowers are typically 5- (occasionally 4- or 6-) merous and have a bicarpellate inferior gynoecium. Invariably, flowers are hermaphrodite and show heterodistyly (also cf. V. Reproductive Biology).

a. CALYX

The calyx is inserted on the roof of the inferior ovary and is mostly comprised of only the free calyx lobes. Rather infrequently (e.g. *D. fragrans*; *P. conspicua*), the calyx lobes are united below to form a (very) short tubular part.

Danais, *Schismatoclada* and *Payera* show general agreement in the shape and size range variation of the calyx lobes. The latter are often \pm triangular, lanceolate to linear-lanceolate. Sizes range from less than 0.5 mm to ca. 10 mm.

In *Danais*, small, broadly to narrowly triangular calyx lobes (less than 0.5 mm to ca. 3 mm long) predominate; longer, often linear-lanceolate to \pm filiform calyx lobes are restricted to few taxa (e.g. *D. andribensis* and *D. volubilis*: to 8-9 mm long). Calyces of *Danais* are either glabrous or hairy on the outer and/or the inner side. The presence of colleters is frequent in the sinuses between two adjacent calyx lobes (e.g. *D. volubilis*, Fig. 5, *C*); less commonly, colleters also occur to their margins.

Schismatoclada agrees with *Danais* in calyx lobe sizes and shapes, but the calyces appear to be always glabrous.

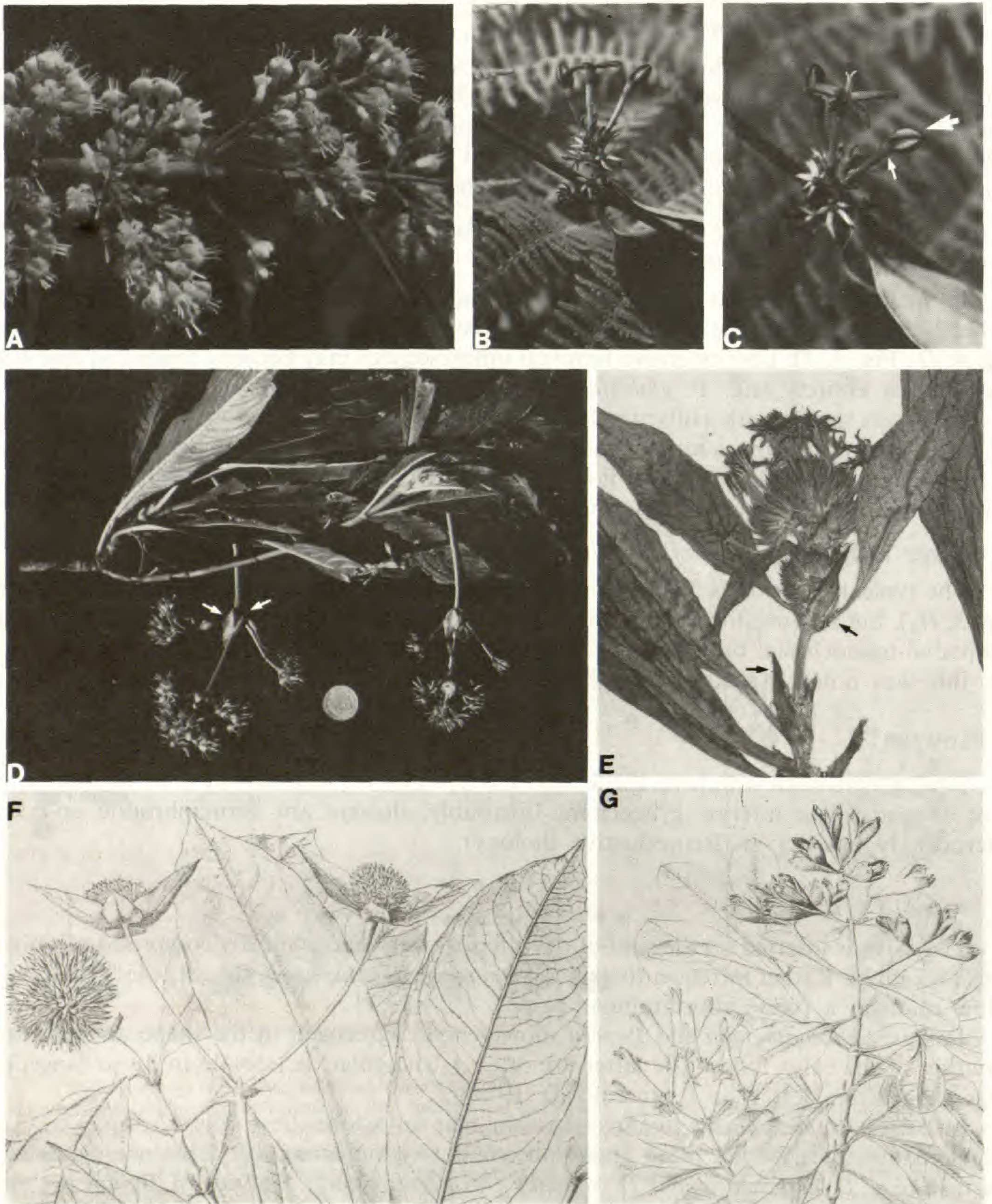


Fig. 4. — A, *Danais fragrans*, short-styled morph. — B-C, *Danais volubilis*, long-styled morph; note valvate-reduplicate aestivation (thick arrow) and widened part of the corolla tube housing the anthers (thin arrow). — D, *Payera decaryi*; note conspicuous bracts (arrows) and compare with F. — E, *P. glabrifolia*, note large stipules (arrows). — F, *P. conspicua*. — G, *Schismatoclada viburnoides*. — F-G reproduced from DRAKE (1898a : plate 450 and 455, respectively).

Although calyx structure in *Payera* is not uniform, there is nevertheless a very clear trend towards very elongated, narrow (linear-lanceolate to \pm filiform) calyx lobes, several times as long as the ovary (cf. Fig. 4, *D-F*). The calyces are mostly hairy.

b. DISK

Taxa of all genera dealt with are characterized by the presence of a ring-like, slightly to conspicuously raised disk inserted on the roof of the inferior ovary.

At least in all species of *Danais* investigated in detail and in *Payera decaryi*, the upper surface of the disk is beset with papillae or short hairs. Numerous idioblasts filled with raphides are found in the interior of the disk (Fig. 5, *F*). In *P. decaryi* it was observed, that the disk tissue also contains sclerenchymatic cells.

c. COROLLA

The entire genus complex is characterized by having a typically 5-merous corolla comprised of a tubular part of varying shape and size and lobes which are arranged in a \pm right angle to the tube or \pm reflexed.

— Corolla tube

Generally, corolla tubes are broadly to narrowly funnel-shaped or cylindrical. In all genera dealt with, the lengths range from a few mm (as little as ca. 2 mm : e.g. *D. breviflora*, *P. bakeriana*) to ca. 20 mm (e.g. *D. coronata*, *S. viburnoides*); in *Payera* and *Schismatoclada*, tubes may occasionally be up to ca. 30 mm long (e.g. *P. coriacea*, *S. marojejyensis*). In general, taxa with longer corollas always have \pm strictly cylindrical tubes (also see Reproductive Biology, below).

It is particularly noteworthy that in several (but not all) species of *Danais* (e.g. *D. breviflora*, *D. coronata*, *D. humblotii*, *D. rhamnifolia*, *D. tsaratananensis*), *Schismatoclada* (e.g. *S. humbertiana*) and *Payera* (e.g. *P. coriacea*, *P. decaryi*), corolla tubes have basal splits (Fig. 5, *C-D*). These short splits (1 mm or less long) are always found near the very base of the corolla tube and represent gaps between two adjacent, otherwise fused petals.

The occurrence of such corolla tube splits (recorded for the first time for the genera in question) is also known from a number of other *Rubiaceae* (see survey of “basal corolla tube fenestrations” in ROBBRECHT, 1988; compare also illustrations in PUFF & IGERSEIM, 1991).

In all genera dealt with, the inner surface of the corolla tube is mostly hairy. Especially in *Danais*, the indumentum particularly in the region of the throat is often very dense : white or whitish, rather long, uniseriate and unicellular hairs are present which frequently extend from the throat and obscure the entrance to the tube (e.g. *D. fragrans* : short-styled flowers; see also Reproductive Biology, below).

As regards the external indumentum of the corolla, there are differences between the genera. In *Danais* and *Schismatoclada*, the outside of the corollas, in general, is glabrous or nearly so (there are, however, exceptions : e.g. morphs of *D. pubescens* which may have a pronounced outer corolla indumentum; *S. villiflora*, with long hairs on the outside of the corolla lobes). *Payera*, in contrast, is characterized by corollas (corolla tubes) whose outside is “silvery hairy”, i.e., densely covered with adpressed, silvery-white hairs.

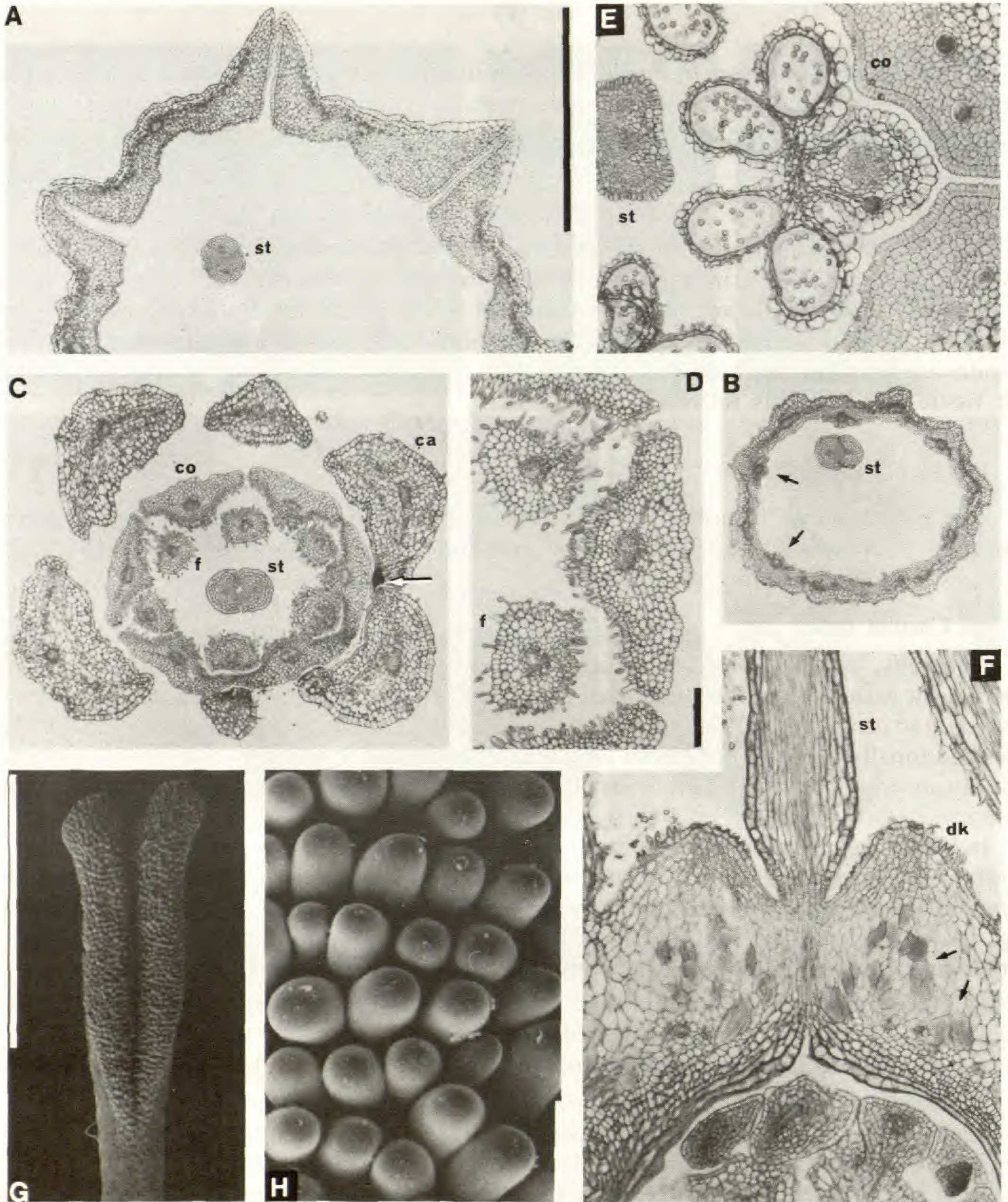


Fig. 5. — Floral anatomy and style and stigma of *Danais* (E-F, *D. fragrans*, all others *D. volubilis*): A-D, bud shortly before anthesis (long-styled morph), sections at different levels; A, in the region of the corolla lobes, note valvate-reduplicate aestivation; B, approximately mid-tube, note filament-like tissue fused to the corolla tube (arrows); C-D, near base of tube, note corolla tube splits and free filaments (f), the arrow points to a sectioned colleter (in the sinus between two calyx lobes, ca); D, detail of C; E, cross section of anther; F, longitudinal section through apical part of ovary (shortly before anthesis), note disk (dk) with raphide containing idioblasts (arrows); G, SEM-graph of uppermost part of style and stigma lobes (from short-styled morph); H, detail of G, stigmatic papillae. — co, corolla; st, style. — Scale bars: 1 mm (A = B = C; D = E = F; G); 50 μ m (H). — Further explanations in the text.

— Corolla lobes

In *Danais* and *Schismatoclada*, the aestivation of the corolla lobes is valvate-reduplicate, i.e., the margins of adjacent lobes are bent outward in bud (cf. Fig. 4, *B-C*; 5, *A*). In contrast, *Payera* has valvate aestivation in the strict sense (cf. ROBBRECHT, 1988 for a survey of aestivation types in the *Rubiaceae* and their definition).

Corolla lobes, generally oblong or \pm elliptic- to linear-lanceolate in shape, do not exhibit any significant differences between the three genera.

d. ANDROECIUM

As all genera dealt with here are heterodistylous (cf. Reproductive Biology), two floral morphs are present : one with anthers long exserted (stamens with long, filiform filaments), the other with the entire stamens included in the corolla tube (almost sessile anthers).

It is noteworthy that — below the actual point of insertion of the free filaments to the corolla — filament-like tissue strands, attached to the inner tube surface (cf. Fig. 5, *B*), can be traced all the way down to the base of the tube (as, for example, in *Paederia*; cf. Figs. in PUFF & IGRSHEIM, 1991). In taxa with basal corolla tube splits, free strands are again seen immediately inside the splits (Fig. 5, *C-D*). In contrast to numerous *Rubiaceae*, vascular supply of the filaments is not fully immersed in the corolla tube tissue.

The anthers are elongate (length to width ratio $> 2 : 1$) and mediodorsifixed throughout. Anther structure (Fig. 5, *E*) agrees with that found in the majority of other *Rubiaceae*. There are two thecae with two pollen sacs each; the pollen sacs, differing slightly in size and arranged somewhat asymmetrically, dehisce lengthwise; conspicuous connective processes are absent.

e. GYNOECIUM

The gynoecium of *Danais*, *Schismatoclada* and *Payera* is, without exception, bicarpellate. There is always a common (fused) style and two \pm filiform stigmatic branches.

The two stigma lobes are beset with roundish papillae (Fig. 5, *G-H*). Due to the presence of heterodistyly (cf. Reproductive Biology), stigmas and upper style portion are either exserted or both style and stigmas remain included in the corolla tube.

Microtome sections of both style and stigma tissue of *Danais spp.* always revealed the presence of raphide-containing idioblasts and a well developed styler canal in the basal part of the style.

— Ovary (Fig. 6, 9)

There is no fundamental difference in ovary structure between *Danais*, *Schismatoclada* and *Payera*. A massively developed septum causes the ovary to become bilocular. There is a large, peltate placenta with numerous ovules in each locule. The placenta is inserted on the septum itself, the area of insertion is long, encompassing at least a third of the length of the entire septum.

In *Payera* and *Danais*, for which detailed data based on either microtome sections or a combination of both SEM and LM investigations are available, the placenta is \pm heart-shaped due to a \pm V-shaped vertical notch in its apical part (clearly visible the tangential sections of locules; cf. Fig. 6, *A*). Corresponding cross sections reveal that the placenta is

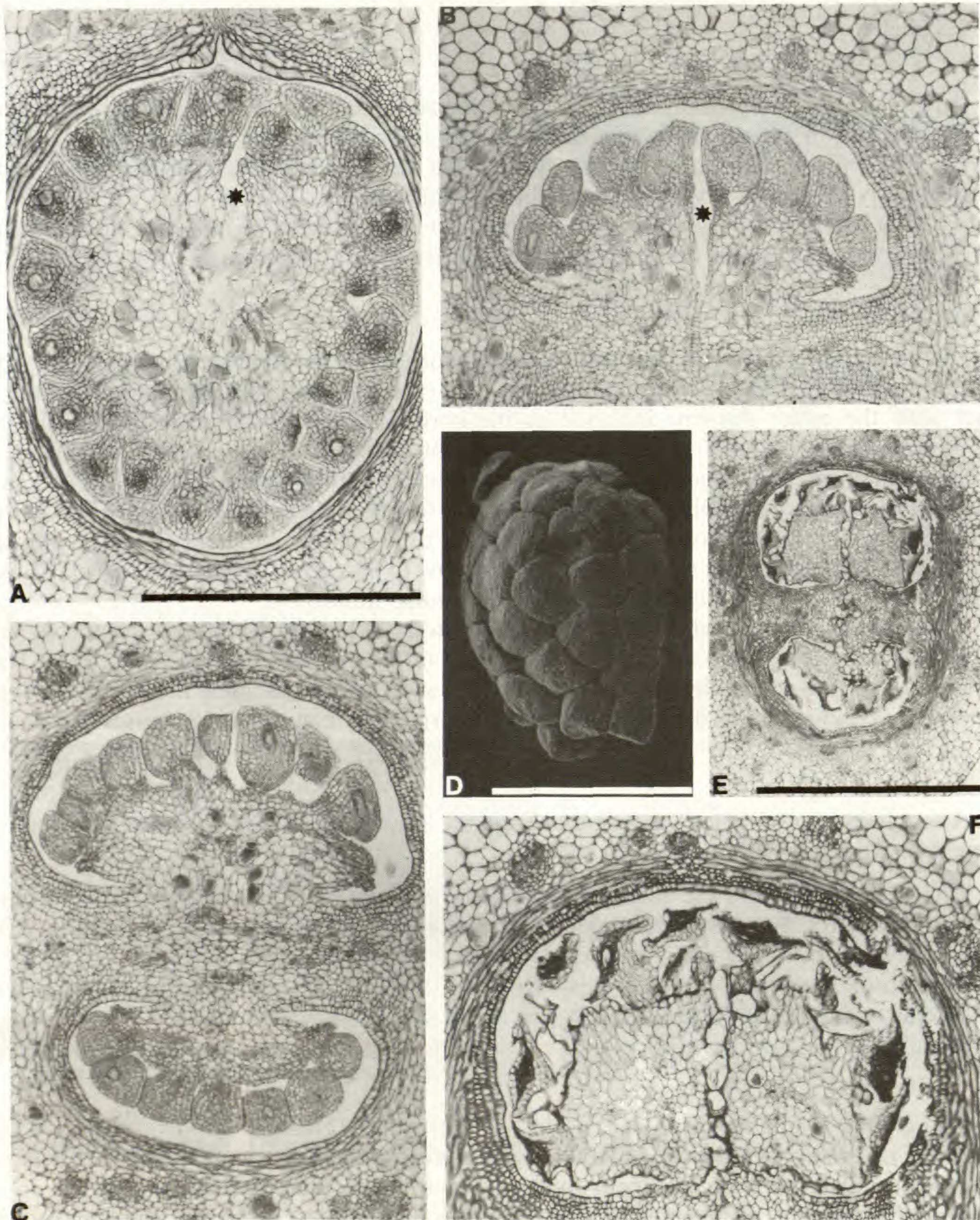


Fig. 6. — Ovary and fruit of *Danais fragrans* : **A**, tangential section of ovary shortly before anthesis, note the V-like notch (*) in the upper part of the placenta (compare with **B**); **B-C**, same developmental stage as **A**, cross sections at different levels, **B**, from upper third of ovary, **C**, from about the middle; **D**, SEM-graph of removed placenta covered with ovules; **E-F**, cross sections from the upper third of immature to \pm mature fruit; note split in the placenta and large, loose cells in the septum (loculicidal dehiscence!). — Scale bars : 1 mm (**E**); 0.5 mm (**A** = **B** = **C** = **F**; **D**). — Further explanations in the text.

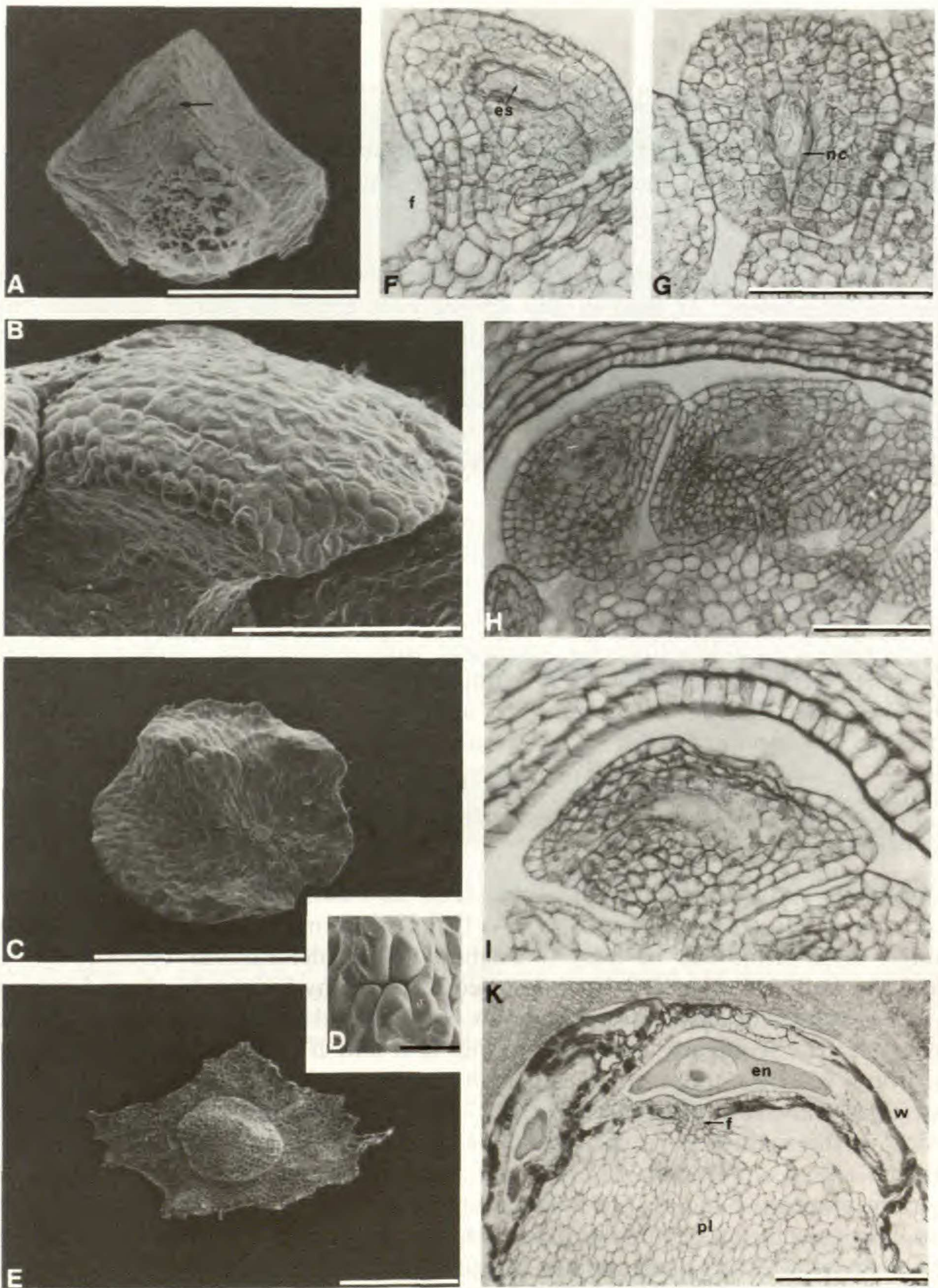


Fig. 7. — Development of the ovule of *Danais fragrans* : A-E, SEM-graphs; A, young ovule from below, the arrow points to the micropyle; B, same developmental stage as A, side view; C, immature seed from below; D, detail of C, showing micropyle; E, mature seed from above. — F-K, LM documentation; F-G, longitudinal and tangential sections of ovule, same developmental stage as A; H, portion of placenta with a few ovules, note beginning development of the wing, I, as H, detail; K, portion of a fruit with immature seed (endosperm, en, and embryo not yet fully differentiated, integument layers below the exotesta partially still intact). — es, embryo sac; f, funicle; nc, nucellus; pl, placenta; w, wing. — Scale bars : 1 mm (C; E); 0.5 mm (K); 100 μ m (A; B; D; F = G = I; H).

clearly two-parted in this region (Fig. 6, *B*); in cross sections made further below this is no longer present and the placenta shows a uniform structure (Fig. 6, *C*; 9, *B*). — As will be documented below, the placenta of mature fruits will normally split in the region of this cleft (loculicidal dehiscence from the apex of the fruit downwards; see IV.5. Fruits).

— **Ovules** (Fig. 7, *A-B*, *F-I*)

The ovules are, as characteristic for the *Rubiaceae* as a whole, tenuinucellate and possess a very massive integument. At least in *Danais* (the only genus for which adequate preserved material was available), the ovules are hemianatropous (Fig. 7, *F*). The hardly curved embryo sac is almost perpendicular to the short funicle. The micropylar canal is slightly curved downwards; Fig. 7, *A* and *F* illustrate the position of micropyle in relation to the funicle.

The shape of the ovules changes in the course of floral development. In earlier stages (i.e., in bud) they are still \pm elliptic in side view, as it is characteristic for numerous other multiovulate *Rubiaceae* (Fig. 7, *F*; \pm angular, probably for spatial reasons, if viewed from above or below, Fig. 7, *A*). The ovules soon start developing flattened outgrowths both in the region of chalaza and at the micropylar end. These outgrowths, originating by local divisions in the integument tissue, may either be very symmetrical or \pm asymmetrical (i.e., better developed on one than on the other side; cf. Fig. 7, *H*). Ovules with symmetrical outgrowths may have a shape resembling that of a one-legged table, whereby the “table leg” corresponds to the funicle of the ovule (Fig. 7, *I*; compare with Fig. 7, *C*, immature seed). At or immediately after anthesis, the ovules already approach in shape the winged seeds that are so characteristic for *Danais*, *Payera* and *Schismatoclada* (cf. IV.6. Seeds).

f. THE CARPEL WALL AND ITS DIFFERENTIATION FROM BUD TO MATURE FRUIT STAGE IN **Danais** AND **Payera** (Fig. 8; 9, *A-C*)

Already in early developmental stages (i.e., in bud), the carpel wall shows a clear differentiation into three layers (Fig. 8, *A*). As they correspond to exo-, meso- and endocarp in fruit stage, these terms will be used throughout in the descriptions below.

Both the **exo-** and **mesocarp** are comprised of parenchymatic cells which form a \pm thick layer. At least the exocarp does not undergo very marked changes during the development from ovary to fruit (compare, for example, Fig. 8, *A* and *B*). In some taxa (e.g. *D. volubilis*), the mesocarp becomes squashed during fruit maturation (Fig. 8, *B*); in others, it hardly changes (e.g. *D. humblotii*, *P. decaryi*, Fig. 8, *C-D*; 9). The vascular supply of the ovary/fruit is embedded in the mesocarp parenchyma; the vascular bundles largely run parallel to the longitudinal axis (i.e. vertically). Per carpel, there are typically a dorsal, two lateral, and another two marginal bundles. The bicarpellate ovary/fruit, therefore, basically has 10 main bundles. Due to splitting of bundles, however, their number is very often increased (further splitting of bundles), the actual number is usually higher. On the border between meso- and endocarp, an almost complete ring of idioblasts filled with raphides is present from relatively early stages of development onwards.

The **endocarp** experiences the most drastic changes during development. In bud stage, it is still thin but, nevertheless, recognizable as a few layers of sclerenchymatic cells (e.g. *D. fragrans*, Fig. 6, *A-C*; 8, *A*). With increasing age, the endocarp becomes considerably thicker (Fig. 6, *E-F*; also compare sections of immature and mature fruits of *P. decaryi*, Fig. 9, *A-B*

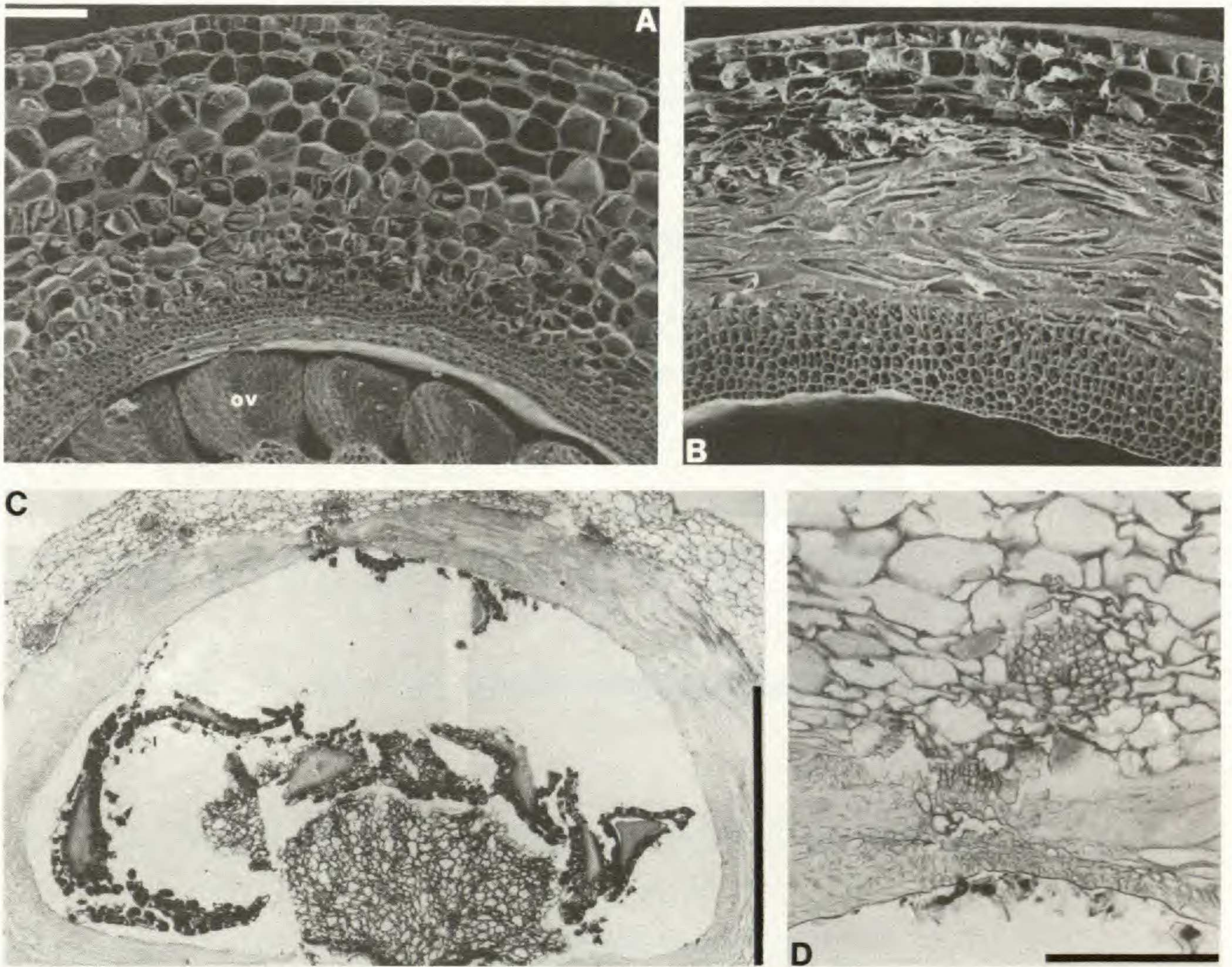


Fig. 8. — Carpel walls of *Danais* species in flower and fruit : **A**, *D. fragrans*, ovary wall at anthesis showing thin endocarp, meso- and exocarp (ov, ovule); **B**, *D. volubilis*, wall of immature fruit showing thick endocarp, partly squashed mesocarp and exocarp; **C-D**, *D. humblotii*, wall of \pm mature fruit; **C**, note very thick, sclerenchymatic endocarp and also placenta and winged seeds in the interior of the locule; **D**, detail of **C**, showing the thin endocarp region on the dorsal side of the carpel where the fruit dehisce. — Scale bars : 1 mm (**C**); 100 μ m (**A = B; D**). — Further explanations in the text.

and **C**). Eventually, it forms a massive to very massive sclerenchymatic layer which, in fully mature fruits, may occur up to ca. 50 % of the entire carpel wall diameter (e.g. *D. humblotii*, Fig. 8, **C**). Also parts of the septum become sclerenchymatic during fruit maturation (cf., for example, Fig. 9, **C**). The endocarp is not uniformly thickened. In the area, where the wall of the fully mature fruits of *Danais* and *Payera* will split open during dehiscence, i.e., on the dorsal side of each carpel, the endocarp is conspicuously thinner-walled; the cross sections reproduced in Fig. 8, **C-D** and 9, **C** illustrate this very well for both *Danais* and *Payera*.

The differentiation taking place in the septum itself is also of interest : from anthesis onwards, few to only one layers of unthickened, large parenchymatic cells are seen in the upper half to third of the septum which run at a right angle to its long axis (cf. Fig. 6, **E**; 9, **A**). These

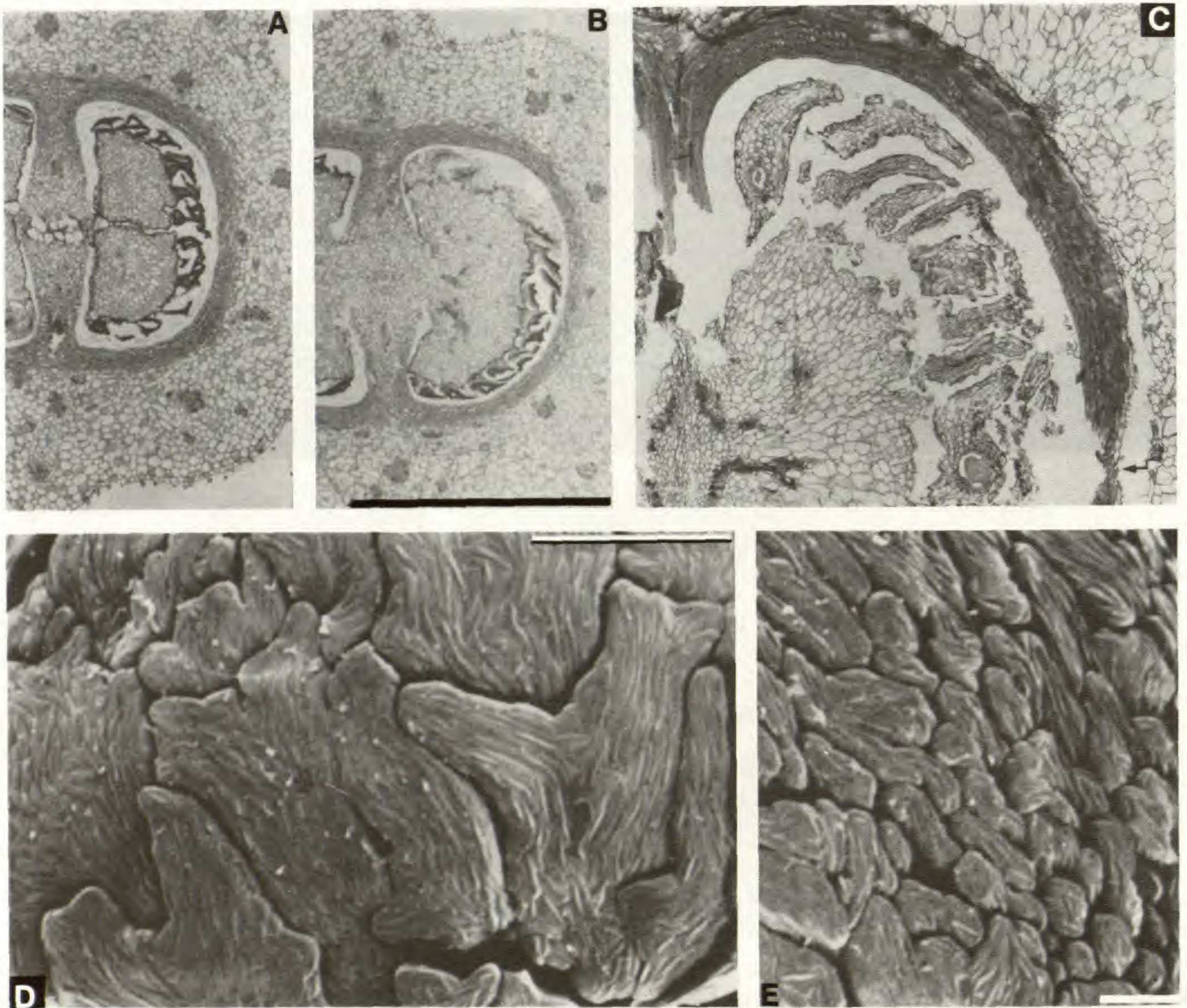


Fig. 9. — Fruit development of *Payera decaryi*: **A-C**, cross sections; **A-B**, of immature fruit, showing septum, locule coated by still thin endocarp, and placenta with developing (and, in part, aborted) seeds; **A**, section from upper third of fruit, note split in the placenta and large, loose cells in the septum (loculicidal dehiscence!); **B**, section approximately mid-fruit, note uniform placenta and septum; **C**, section of almost fully mature fruit, note thick endocarp (arrow: thinner portion, where the fruit will dehisce) and winged seeds; **D**, SEM-graph of developing seeds still attached to the placenta (the latter not visible; removed from a not fully mature fruit), note irregular shapes and asymmetrical wings; **E**, aborted seeds (no wings developed!), from the same preparation as **D**. — Scale bars: 1 mm (**A = B = C**); 0.5 mm (**D**); 100 μ m (**E**). — Further explanations in the text.

cells will remain thin and parenchymatic during maturation and form the region where the septum will break during the (loculicidal) dehiscence of the fruits (see also IV.5. Fruits).

The mature fruits of *Payera* have a conspicuous “beak” (Fig. 10, *I-K*; see also IV.5. Fruits). Its development is intimately linked with the fate of the endocarp during fruit maturation, as the beak is essentially an upward extension of the endocarp (cf. Fig. 10, *K*). Its growth is correlated with the increase in extent of the actual endocarp during fruit maturation. For this reason, immature fruits normally do not yet show a clearly discernible beak (thus

giving the erroneous impression, no beak is developed). It is typically only at a very late stage of development that a beak becomes conspicuous.

Although detailed anatomical investigations of the fruits of *Schismatoclada* (also beaked) are lacking, morphological investigations suggest that there is no fundamental difference.

5. FRUITS (Fig. 10)

In all genera dealt with here, the fruits are capsules which are crowned by the persistent calyx. There are, however, differences in the dehiscence and in details of the fruit structure.

Loculicidal dehiscence is characteristic for the capsules of both *Danais* and *Payera*. The carpel walls break open dorsally (i.e., at right angles to the septum) from the top to about the middle or to the lower third of the fruit (Fig. 10, *A*, *C-D*). At the same time, also the septum splits from the top downwards; normally, at least parts of the placentas, too, \pm separate into two halves.

The two genera also show general agreement in the typically globose or \pm globose shape of their glabrous or \pm hairy capsules. In the relatively large genus *Danais*, there is, however, some variation: *D. vestita*, for example, has rather distinctly invertedly heart-shaped fruits; sometimes there is a trend to fruits which are slightly wider than long; occasionally, fruits are somewhat compressed laterally (i.e., at right angle to the septum; e.g. *D. vestita*), and there may be \pm conspicuous constrictions in the area of the septum (e.g. *D. volubilis*, Fig. 10, *B*).

Fruits of *Payera* tend to be small, i.e., often ca. 3-6 mm in diam., those of *Danais* show much variation in size (sometimes even within species). Diameter or greatest lengths of fully mature fruits of *Danais* range from only ca. 2-3.5 mm (e.g. *D. rhamnifolia*, *D. microcarpa*, or *D. ligustrifolia*) to ca. 8-15 mm (e.g. *D. coronata*, *D. volubilis*).

Only in a single species of *Danais* (*D. aurantiaca*), postgenital fusions of immediately adjacent fruits were noted regularly. Most commonly observed were groups of three fruits (ultimate inflorescence elements: three-flowered cymes!) which are fused together in their lower third. Normally, also their pedicels, \pm woody and flattened in fruiting stage, become part of this fusion (Fig. 10, *D*).

Finally, a marked difference between the two genera with loculicidally dehiscent fruits needs to be pointed out: In *Payera*, the capsules are distinctly "beaked", i.e., they show a marked apical projection inside the persistent calyx lobes (cf. *P. decaryi*, Fig. 10, *I-K*). In contrast, fruits of *Danais* always lack a conspicuous "beak", i.e., the fruit apex is \pm rounded (cf. *D. volubilis*, Fig. 10, *A-B*).

Septicidal dehiscence is characteristic for the capsules of *Schismatoclada*. The fruits, moreover, typically are \pm strongly elongated (\pm ellipsoid or ovoidal); they are often ca. 7-15 mm long and 4-7 mm wide and mostly glabrous.

Schismatoclada, like *Payera*, has "beaked" fruits (e.g. *S. psychotrioides*, Fig. 10, *E-H*). In dehiscent fruits, the beak itself may — especially if it is relatively long — also split and become bilobed (Fig. 10, *G-H*). This loculicidal split of the beak is a secondary event: during septicidal dehiscence of a fruit, the lateral portions of each carpel wall start bending outward, thus causing the sclerenchymatic, inflexible beak to rupture.

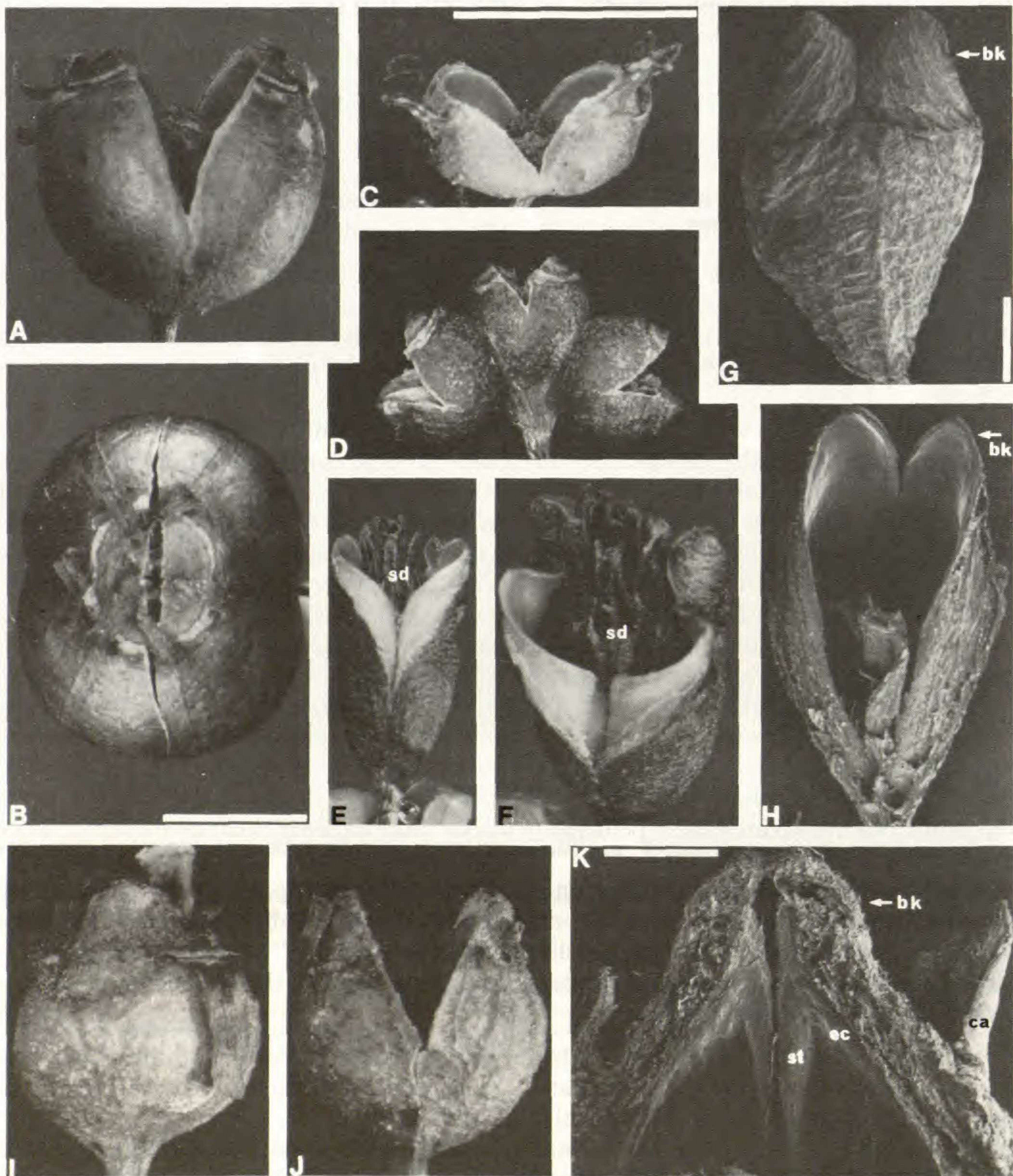


Fig. 10. — Fruits of A-D, *Danais*, E-H, *Schismatoclada* and I-K, *Payera* : A-B, *D. volubilis*, side view and from above, note absence of "beak" and loculicidal dehiscence; C, *D. ligustrifolia*; D, *D. aurantiaca*, note that fruits are fused together basally; E-H, *S. psychotrioides*, E-F, note septicidal dehiscence and seeds (sd) protruding from the apex, G, dorsal view of carpel, H, ventral view (septum removed), note that the beak also splits loculicidally; I-K, *P. decaryi*, I, side view, J, loculicidally dehiscent fruit, K, view of inner side of dehiscent fruit, note septum (st) and endocarp (ec) extending into the beak. — bk, beak; ca, calyx lobe. — Scale bars : 5 mm (A = B = D = E; C = F = I = J); 1 mm (G = H; K).

6. SEEDS (Fig. 7, E, K; 11-14)

The entire genus complex is characterized by **winged seeds**. There are, however, marked differences in wing structure (size, shape, exotesta cells), so that the genera in question will be dealt with separately.

Danais

The seeds are characterized by having basically \pm circular to slightly asymmetrical, elongated-circular wings. The latter are produced around the \pm centrally located endosperm- and embryo-bearing part of the seed which, in turn, is compressed-spherical in shape (e.g. *D. rhamnifolia*, Fig. 11, A). The hilum is mostly found in a region corresponding \pm to the geographic middle of the central endosperm- and embryo-bearing part of the seed (Fig. 7, K; *D. coronata* : compare Fig. 11, E and F); sometimes, however, it is shifted to below the middle (cf., for example, *D. ligustrifolia*, Fig. 11, C). The actual wing margins are often quite irregularly shaped and lacerate (e.g. *Danais rhamnifolia*, *D. ligustrifolia*, Fig. 11, A-C). The wings themselves invariably are thin (cf. Fig. 12, D and Seed Anatomy, below!).

There are interspecific differences with regard to seed size, seed wings and shape and size of the exotesta cells in the wing region; also a certain amount of intraspecific variation was observed in some species. Exotesta cells in the wing region vary in shape from conspicuously elongated (\pm narrowly rectangular; most common) to \pm square and polygonal (cf. Fig. 11, D, G; 12, C, E); within one and the same seed wing, cells not uncommonly do show some variation in shape.

Diameter or greatest lengths of well developed (presumably viable) seeds (incl. the wings) range from only ca. 0.6 to 6 mm. *D. rhamnifolia* is an example for a species with small seeds (ca. 0.6-1 mm) with relatively indistinct, small wings, *D. coronata* an example for a species with large seeds (ca. 4-6 mm) with very conspicuous wings (Fig. 11, E-F).

Concerning the seeds and their wing size and shape, the following frequently made observation is important : aborted, non-viable seeds (usually easily recognized by the poorly developed, very small central seed area which normally houses the endosperm and embryo) always also develop wings. Such "pseudo-seeds" tend to be smaller than and also differ in wing size and shape from viable seeds. Investigation of "pseudo-seeds" can yield very misleading and distorted information.

Seed anatomy of Danais (Fig. 12, D, F-G; 13)

In mature seeds, the winged portion is thin (Fig. 12, D). Typically, it is only comprised of the upper and lower exotesta layer. Between them, some crushed remnants of the former massive integument may be discernible (in immature seeds, the cellular structure of these integument layers is normally still intact). The radial walls of the exotesta cells have very prominent secondary thickenings about their middle, which are \pm round to heart-shaped in cross section (Fig. 12, F; 13). The other walls of the exotesta cells, mostly \pm completely collapsed in fully mature seeds, neither have any conspicuous thickenings nor "pits". TEM sections, however, reveal that there are irregularly spaced thickenings in the outer tangential walls (Fig. 13, B-C) which, at present, cannot be interpreted; they are not to be seen in the

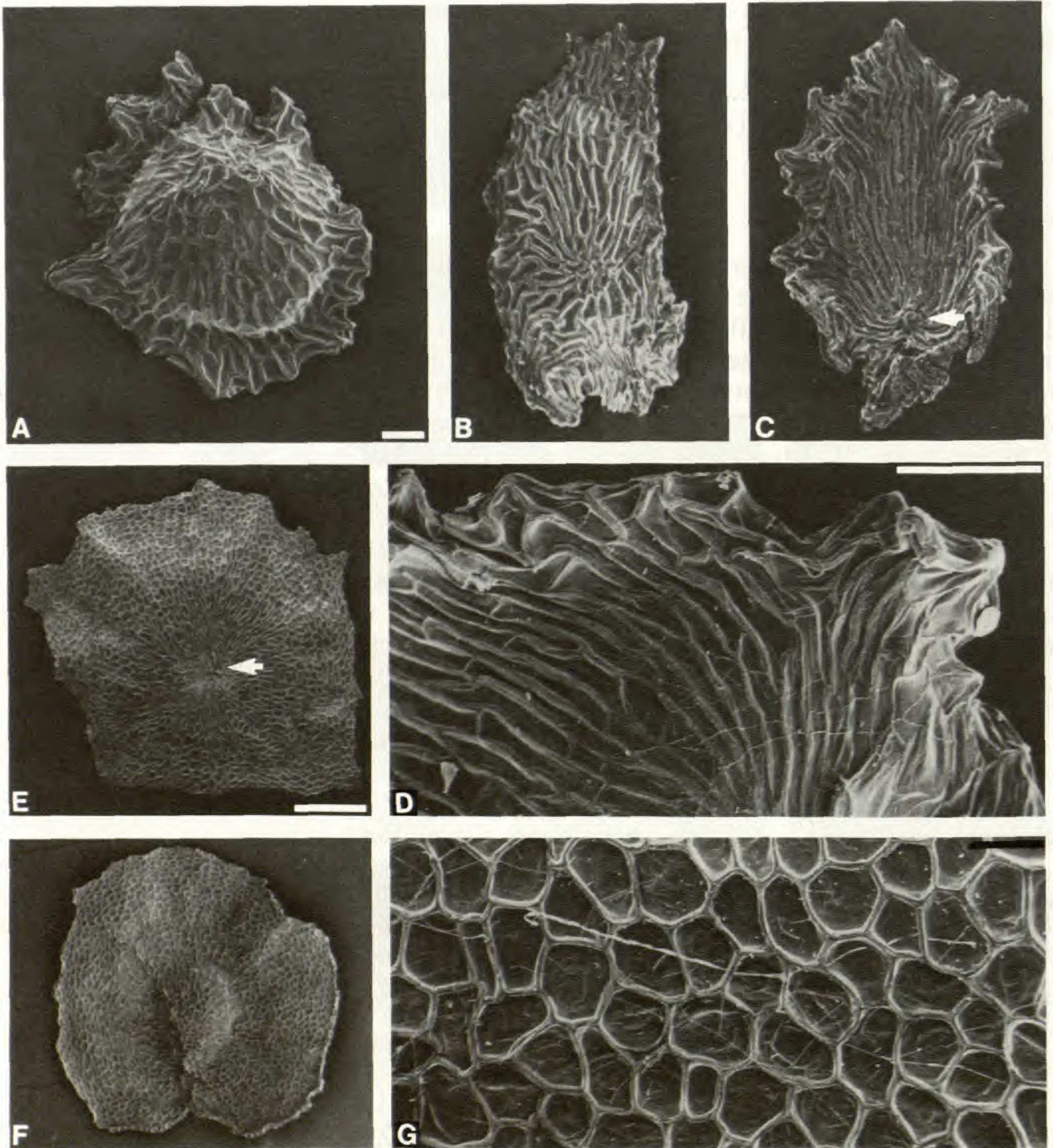


Fig. 11. — Seeds of *Danais* species : A, *D. rhamnifolia*, from above; B-D, *D. ligustrifolia*; B, from above; C, from below; D, detail of seed wing; E-G, *D. coronata*; E, from below; F, from above; G, detail of seed wing. — The arrows (C, E) point to where the seeds have broken off from the placenta. — Scale bars : 1 mm (E = F); 100 μ m (A = B = C; D; G).

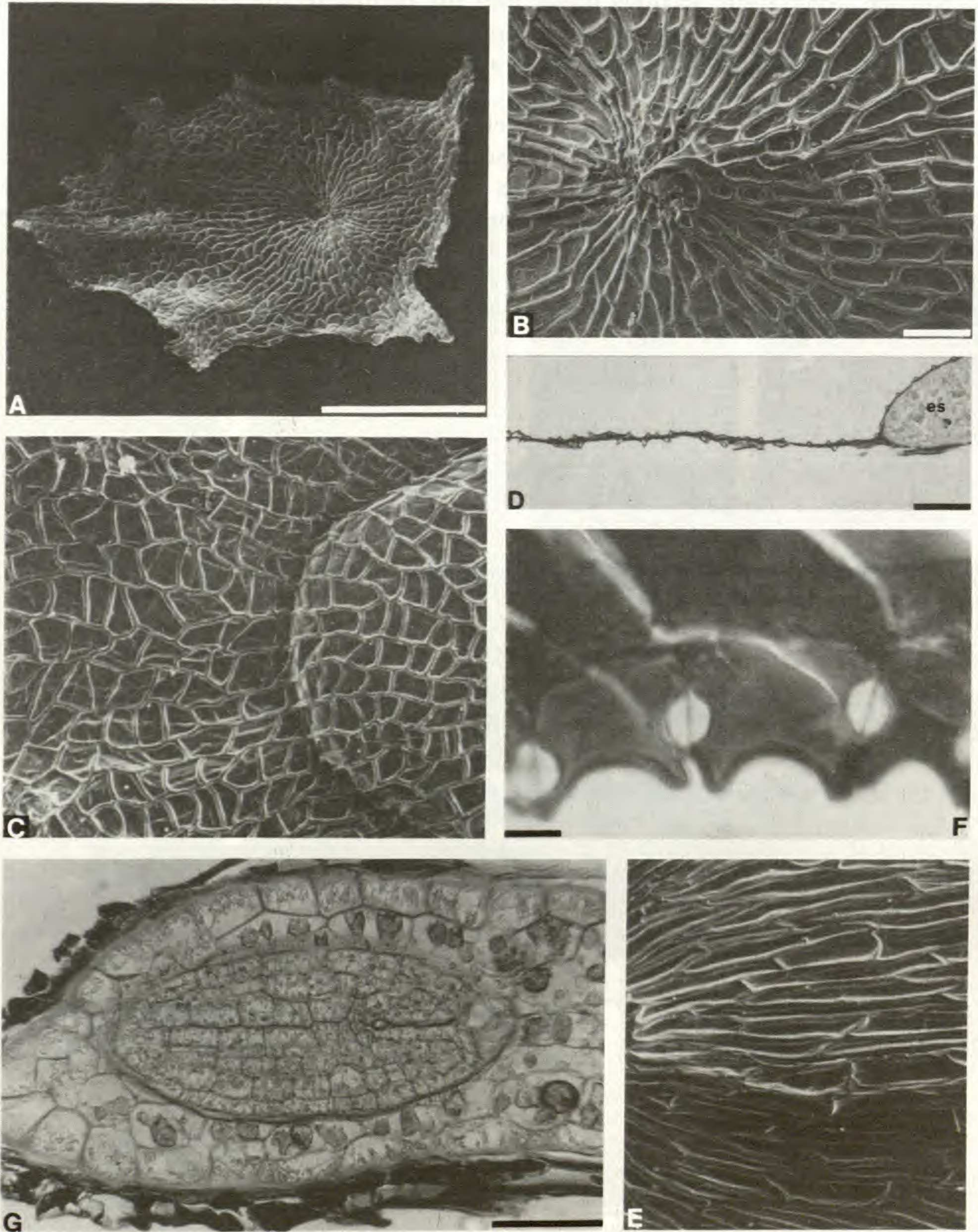


Fig. 12. — Seeds of *Danais* species : **A-D**, *D. fragrans* ; **A**, from below ; **B**, detail of **A**, showing the point of insertion on the placenta ; **C**, detail of a seed as seen from above ; **D**, cross section of seed, \pm corresponding to the portion shown in **C** ; a segment of the central, endosperm (es) and embryo bearing part is seen on the right, the thin wing on the left. — **E-F**, *D. pubescens* ; **E**, detail of seed wing ; **F**, section of exotesta cells showing secondary thickenings (white) in the radial walls. — **G**, *D. ligustrifolia*, cross section of the central part of a not fully mature seed showing a proembryo in the centre. — Scale bars : 1 mm (**A**) ; 100 μ m (**B = C = E ; D**) ; 50 μ m (**G**) ; 10 μ m (**F**).

light microscope. Microtome sections reveal that the lumina of the exotesta cells of mature seeds are filled with excretions (most probably tannins), which are stained dark reddish-brown by safranin; the thickenings of the radial walls, in contrast, appear colour-less (cf., for example, Fig. 12, *F*).

The central part of the seed, \pm round to elliptic in shape when viewed from above (cf. Fig. 11, *A-B*) and elliptic to \pm hemispherical in section (cf. Fig. 12, *G*) contains the endosperm. The latter is comprised of tightly packed cells filled with starch as storage material (oil is absent). The embryo lies \pm parallel to the long axis of the winged seed (hemianatropous orientation of the former ovule; cf. Fig. 12, *G*). Its length equals about a third of the length of the endosperm. The radicle points to the region of the former micropyle and is \pm straight. The cotyledons are small, i.e., only ca. half as long as the radicle.

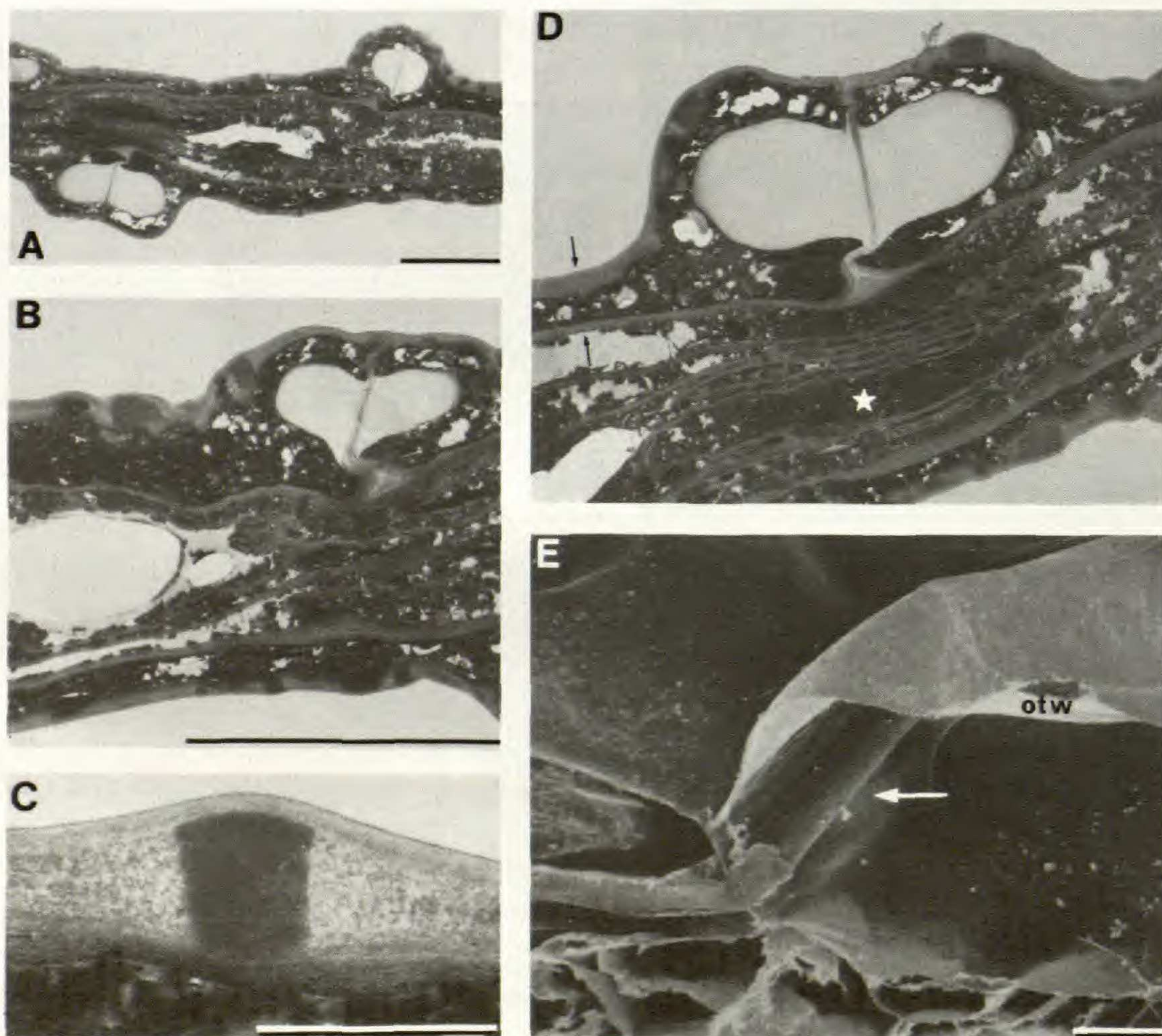


Fig. 13. — Details of the exotesta cells of *Danais*: **A-B, D**, portions of the seed wing showing upper and lower exotesta cells and crushed remnants of parenchymatic cells (*) in between (arrows: inner and outer tangential wall of exotesta cell); **B, D**, note local, massive secondary thickenings (white) in the radial walls; **C**, detail of outer tangential wall with local thickening; **E**, part of exotesta cell from an immature seed showing outer tangential wall (otw) and still rather thin thickening of the radial wall (arrow); **A-D**, *D. fragrans*, TEM-graphs; **E**, *D. volubilis*, SEM-graph. — Scale bars: 10 μ m (**A**; **B = D**; **E**); 1 μ m (**C**).

Schismatoclada (Fig. 14, A)

The seeds of *Schismatoclada* (e.g. *S. psychotrioides*, Fig. 14, A) are always much elongated (length to width ratio at least 4 : 1). They are distinctly bipolar and often have a \pm sagittate appearance. The endosperm- and embryo-bearing part is found immediately above the two relatively small basal tail-like wings. The latter are produced on the micropylar side, to the left

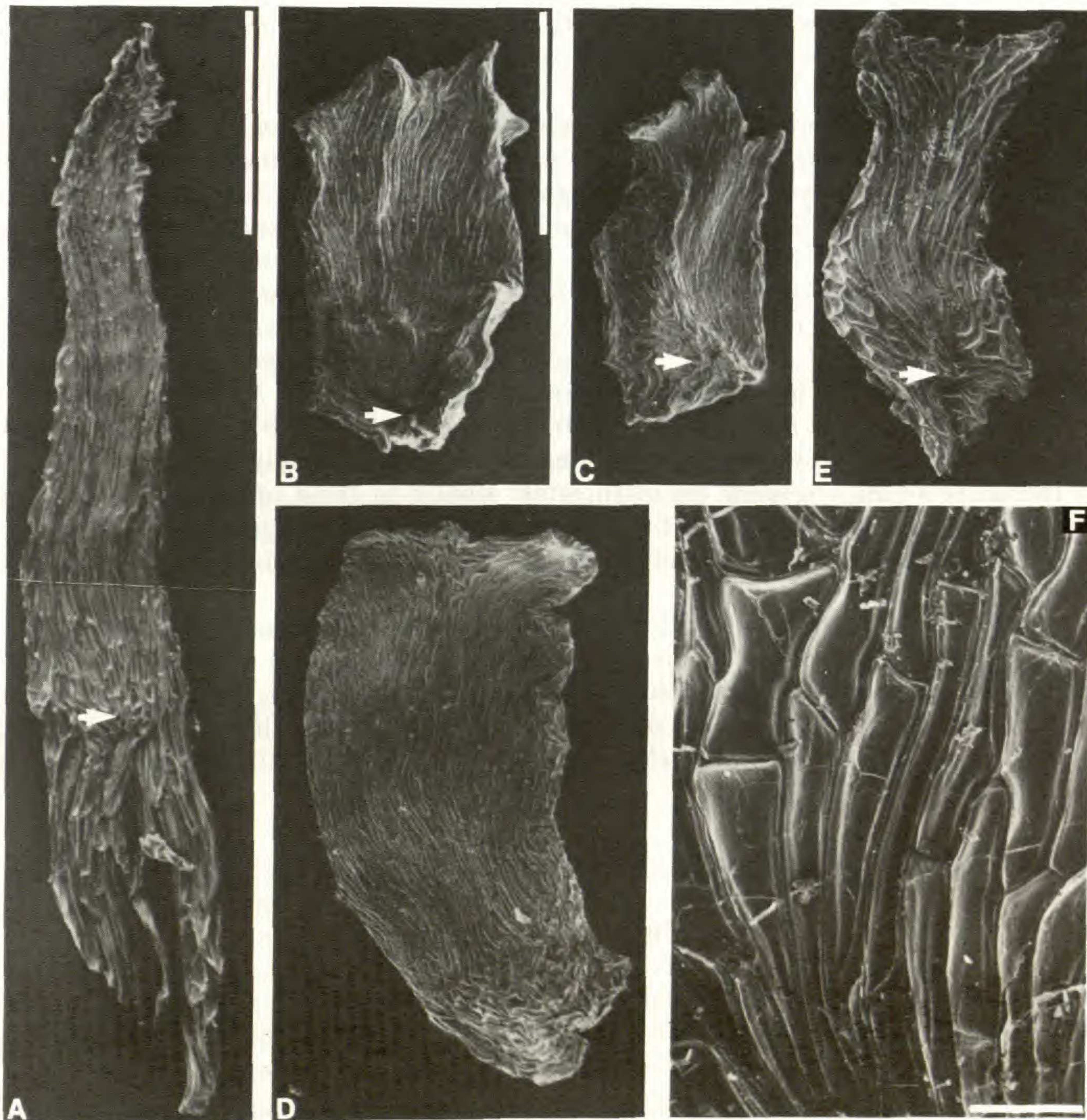


Fig. 14. — Seeds of **Schismatoclada** and **Payera** species : A, *S. psychotrioides*, from below; B-C, *P. bakeriana*, from below, both from the same collection; D, *P. homolleana*, from above; E-F, *P. decaryi*; E, from below; F, detail of seed wing. — The arrows point to where the seeds have broken off from the placenta. — Scale bars : 1 mm (A); 0.5 mm (B = C = D = E); 100 μ m (F).

and to the right of the region of the funicle/hilum. Above the endosperm- and embryo-bearing part of the seed, which is often \pm oblong to elliptic in surface view, is the single apical wing-like appendage. The size ratio of apical wing, endosperm- and embryo-bearing part and basal wings is frequently 1 : 1 : 1.

Seeds of *Schismatoclada* are often ca. 4-5 mm long and ca. 1 mm wide.

In *Schismatoclada*, the exotesta cells in the region of the wings are always much elongated and \pm rectangular. Anatomically, seed wings and exotesta cells do not differ from those of *Danais*.

Payera

The seeds of *Payera* are \pm rectangular to \pm asymmetrical (Fig. 14, B-F). Length to width ratios of the seeds range from ca. 2 : 1 to ca. 3 : 1. As compared to the other two genera, the seeds are small, i.e., only ca. 0.5-2 mm long and 0.3-1 mm wide.

Seeds often do show a certain bipolarity, but this not always very obvious at first sight. Upon closer examination it can be seen that there are — as in *Schismatoclada* — two basal tail-like appendages to the left and to the right of the funicle/hilum which, however, are inconspicuous (cf., for example, Fig. 14, D). As opposed to *Schismatoclada*, the apical wing portion is relatively short and wide; it may be rather irregularly shaped and sometimes show a \pm indistinct bifurcation in its uppermost part (cf. Fig. 9, D; 14, B, E). The endosperm- and embryo-bearing part of the seed is \pm centrally located. The size ratio of apical wing, endosperm- and embryo-bearing part and basal wings is frequently 1 : 1 : 0.5.

The shape of *Payera* seeds are often rather similar to those of certain *Danais* species (compare, for example, Fig. 14, B-E and Fig. 11, B-C, *D. ligustrifolia*).

The exotesta cells in the region of the wings tend to be elongated-rectangular (Fig. 14, F) to \pm square.

In *Payera*, the seed surface often has a “smoother” appearance than in *Danais* or *Schismatoclada*. The reason for this is that the outer tangential walls of the exotesta cells are frequently not completely collapsed, so that the thickened radial walls are not so prominently projected. The secondary thickenings of the radial exotesta cell walls, however, are the same as those found in *Danais* and *Schismatoclada*. Also the small embryos with their small cotyledons agree with the other two genera.

V. REPRODUCTIVE BIOLOGY

1. HETEROSTYLY

Heterodistyly occurs in all genera dealt with here. Whether it actually does occur in every single species is not known because of some taxa only poor material is available. As in the majority of heterostylous *Rubiaceae*, distyly prevails. The two floral morphs are distinguishable at first glance : in long-styled flowers, style and stigmas are conspicuously exerted and stamens entirely included; in short-styled flowers, the long filaments and the anthers are

exserted whereas style and stigmas are hidden in the corolla tube. In a rubiaceous context, the situation is termed “complete heterostyly” (as opposed to “incomplete heterostyly”; cf. ROBBRECHT, 1988).

In addition to these very obvious differences, there are other noteworthy details in which long- and short-styled morphs differ.

1. *Corolla tube shape dimorphism due to heterodistyly*

This seems to be very pronounced only in *Danais* where, in long-styled morphs (especially of taxa with relatively narrow tubes such as *D. volubilis* or *D. coronata*), the tubes are often conspicuously widened in the region where the anthers are located (cf. Fig. 4, B-C). In short-styled morphs of the respective species, tubes are continuously cylindrical and lack a widened upper portion. It, moreover, was observed in most taxa of *Danais* that the indumentum in the region of the throat differs a little to very markedly in long- and short-styled flowers. The most common situation is that, in one and the same species, throats are densely pilose in long-styled flowers but mostly only sparsely hairy in short-styled flowers (e.g. *D. fragrans*; *D. xanthorrhoea*: VERDCOURT, 1976). An identical heterostyly-linked dimorphism in the corolla indumentum was also observed in *Payera* (e.g. *P. coriacea*) and noted for *Schismatoclada thouarsiana* (CAVACO, 1967).

2. *Differences in the stigma lobe micromorphology*

In all three genera investigated, the stigmatic branches of long-styled flowers are spreading to recurved and relatively thick. In short-styled flowers, stigma lobes are in close vicinity to each other, erect and thinnish (cf. Fig. 5, G). It appears that number, shape and size of stigmatic papillae also differ between long- and short-styled morphs.

3. *Pollen exine dimorphism due to heterodistyly*

This phenomenon was noted in all three genera investigated and will be dealt with in detail in chapter VI. Pollen.

2. NOTES ON THE POLLINATION ECOLOGY OF *Danais*

Although actual field observations are very fragmentary, a number of interesting details can be reported on species of *Danais*:

Particularly the long-tubed *Danais* species, namely *D. coronata*, *D. dauphinensis*, *D. nigra*, *D. pauciflora* and *D. volubilis* (cf. Fig. 4, B-C), appear to be of special interest. They are the only taxa in the genus in which the cylindrical corolla tubes and the in- and outside of the spreading to \pm recurved corolla lobes are whitish to olive green (*D. dauphinensis*), dark-purple or -brown, dark brown-olive to almost black (the other four species). These species are likely to be phalenophilous. According to VOGEL (1954), such phalenophilous blossoms are distinguished from hawkmoth flowers (sphingophilous blossoms), inter alia, by their inconspicuous colour, smaller flower sizes (shorter corollas) and narrow tubes, in which nectar is hidden at a depth of ca. 4 to 20 mm. All of these characteristics also apply to the five mentioned *Danais* species. VOGEL (1954), furthermore, noted that phalenophilous blossoms are

to emit a strong, perfume-like scent at night. In *D. volubilis*, the only species of this group observed in the field, no obvious scent was noticed, but the population was visited in the morning (ca. 9 a.m.), i.e., at a time when scent production might have already ceased.

The remaining taxa of *Danais* have flowers in which the upper (morphologically inner) surface of the mostly spreading to \pm recurved corolla lobes is yellowish, yellow-orange, orange, orange-red as well as pure red (in contrast, the outside of the lobes and the corolla tubes tend to be more inconspicuously coloured, i.e., greenish-yellow, greenish, etc.). Within taxa with predominantly orange-red flowers there apparently are sometimes also whitish morphs. Moreover, changes in flower colour seem to be quite frequent; corollas that are yellow or yellow-orange at first become markedly darker (orange-red, red) before they drop off. Within this group, there appear to be both melitto- and sphingophilous species. It is presumed that species with rather short and relatively wide corolla tubes (e.g. *D. fragrans*, cf. Fig. 4, A) are pollinated by bees, while those with relatively longer, narrower tubes and typical infundibuliform corollas are more likely pollinated by butterflies (e.g. *D. vestita*). A fragrant odour has occasionally been recorded on herbarium sheets for several of the presumably melittophilous species (e.g. *D. fragrans*, *D. ligustrifolia* and *D. rhamnifolia*); no mention is made of any odours for taxa with presumably sphingophilous species (it should be noted, however, that information on herbarium labels, in general, is scanty). The distinction between the two does not always seem to be very clear-cut. Confirmation by field observations is needed.

Data available on *Schismatoclada* and *Payera* are hardly sufficient for an evaluation. In both, flower colours range from white, yellowish, red to purplish. Corolla tube shapes and sizes largely agree with the range of variation found in *Danais*. It might be speculated that both genera contain at least melitto- and psychophilous, and possibly also sphingophilous taxa (species with corolla tubes to ca. 30 mm long, such as *P. coriacea* and *S. marojejyensis*).

VI. POLLEN (Fig. 15-17; Table 3)

The pollen grains of *Danais* are 3-5-colporate and those of *Schismatoclada* and *Payera* 3-4-colporate. In all three genera, grains are spheroidal to subspheroidal and have relatively long and narrow colpi.

The sizes of the pollen grains range from 10 to 30 μm (Wodehouse preparations — cf. Material and Methods; Table 3); in subspherical grains, P and E values normally only differ by 1 to 3 μm . Both *Danais* and *Payera* exhibit much variation in pollen grain size (10 to 26 μm and 15 to 30 μm , respectively); the values for *Schismatoclada* are \pm intermediate (18-22 μm).

Within *Danais*, there seems to be some correlation between pollen grain size and the number of colpi present: taxa with invariably 3- or 3(-4)-colporate grains (e.g. *D. fragrans*, *D. ligustrifolia*, *D. rhamnifolia*) tend to have smaller grain sizes (ca. 10 to 18 μm , less often to 20 μm), those species with 4(-5) colpi (e.g. *D. volubilis*, *D. coronata*) larger grains (20 μm or more); cf. Table 3 and compare Fig. 15, F and H.

TABLE 3 : Selected palynological characters of **Danais**, **Schismatoclada** and **Payera**. — Colp. : number of colpi. — Size range of pollen from long- (LS) and short-styled morphs (SS) : minimum and maximum sizes in μm (since the pollen grains are spheroidal to subspheroidal, P/E values are not given separately); measurements of pollen from Wodehouse preparations. — Dimorph. : “yes” means that SEM investigations revealed the presence of heterostyly-linked pollen *exine* dimorphism (see text!); the question mark indicates that no SEM data are available.

Taxon	Colp.	Size range (LS)	Size range (SS)	Dimorph.
<i>Danais</i> :				
— species with 3- or 3(-4)-colp. grains				
<i>D. aurantiaca</i>	3(-4)	10-14		?
<i>D. breviflora</i>	3		11-14	?
<i>D. cernua</i>	3(-4)	10-16	12-16	?
<i>D. corymbosa</i>	3(-4)		16-20	?
<i>D. fragrans</i>	3(-4)	11-14	14-18	yes
	3	“small” ¹	“small” ¹	?
<i>D. humblotii</i>	3	12-16	14-16	?
<i>D. ligustrifolia</i>	3(-4)	12-15	13-15	yes
<i>D. microcarpa</i>	3	11-16	15-18	yes
<i>D. pubescens</i>	3	12-16	13-18	?
<i>D. rhamnifolia</i>	3(-4)		12-14	yes
<i>D. tsaratananensis</i>	3(-4)	14-20	16-18	?
<i>D. xanthorrhoea</i>	3(-4)	12-14	12-14	yes
— species with 4(-5)-colp. grains				
<i>D. coronata</i>	4(-5)	20-22	20-22	yes
<i>D. nigra</i>	4(-5)		22-26	?
<i>D. volubilis</i>	4(-5)	22-24	23-26	yes
Danais (total)	3-5	10-24	11-26	
<i>Payera</i> :				
<i>P. bakeriana</i>	3(-4)	18-22		?
<i>P. beondrokensis</i>	4	24-28	28-30	?
<i>P. decaryi</i>	3	15-17		?
<i>P. [Coursiana] homolleana</i>	4	15-18		yes
<i>P. madagascariensis</i>	4	19-21		?
<i>P. mandrarensis</i>	4	20-26		yes
Payera (total)	3-4	15-28	28-30	
<i>Schismatoclada</i> :				
<i>S. citrifolia</i>	3-4 ¹	“small” ¹	“small” ¹	?
<i>S. humbertiana</i>	3	20-22		?
<i>S. marojejyensis</i>	4		18-22	?
<i>S. psychotrioides</i>	4		18-22	yes
<i>S. psychotrioides</i>	“mostly 3” ²	“small” ²		
	“mostly 4” ³		“small” ³	
Schismatoclada (total)	3-4	20-22	18-22	

1-3. Data from LEWIS (1965); 1 “small” *sensu* ERDTMAN [“1952” = (1971)], i.e. 10-25 μm ; not specified whether from long- or short-styled morph; based on measurements of acetolysed pollen. 2-3 refers to long- and short-styled morphs, respectively. — See also text!

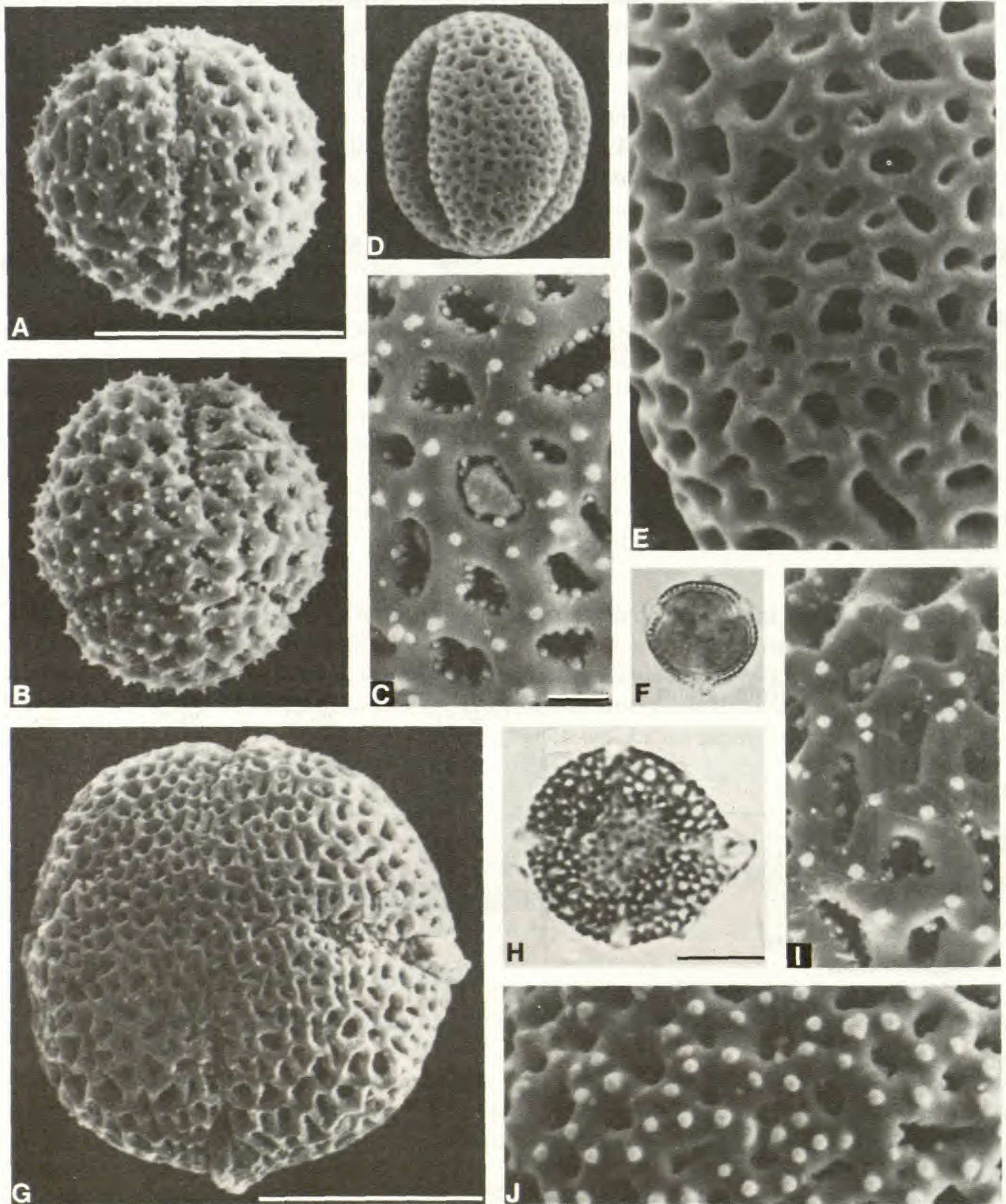


Fig. 15. — Pollen of *Danais* species : **A-F**, *D. fragrans*, **A-C**, short-styled, and **D-F**, long-styled morph; **A**, **D**, equatorial views; **B**, polar view; **C**, detail from polar region; **E**, detail of mesocolpium; **F**, polar view, LM-graph; **G-I**, *D. volubilis*; **G-H**, long-styled morph, polar views, SEM- and LM-graphs; **I**, short-styled morph, detail of mesocolpium; **J**, *D. rhamnifolia*, short-styled morph, detail of mesocolpium. — Scale bars : 10 μm (**A** = **B** = **D**; **F** = **H**; **G**); 1 μm (**C** = **E** = **I** = **J**).

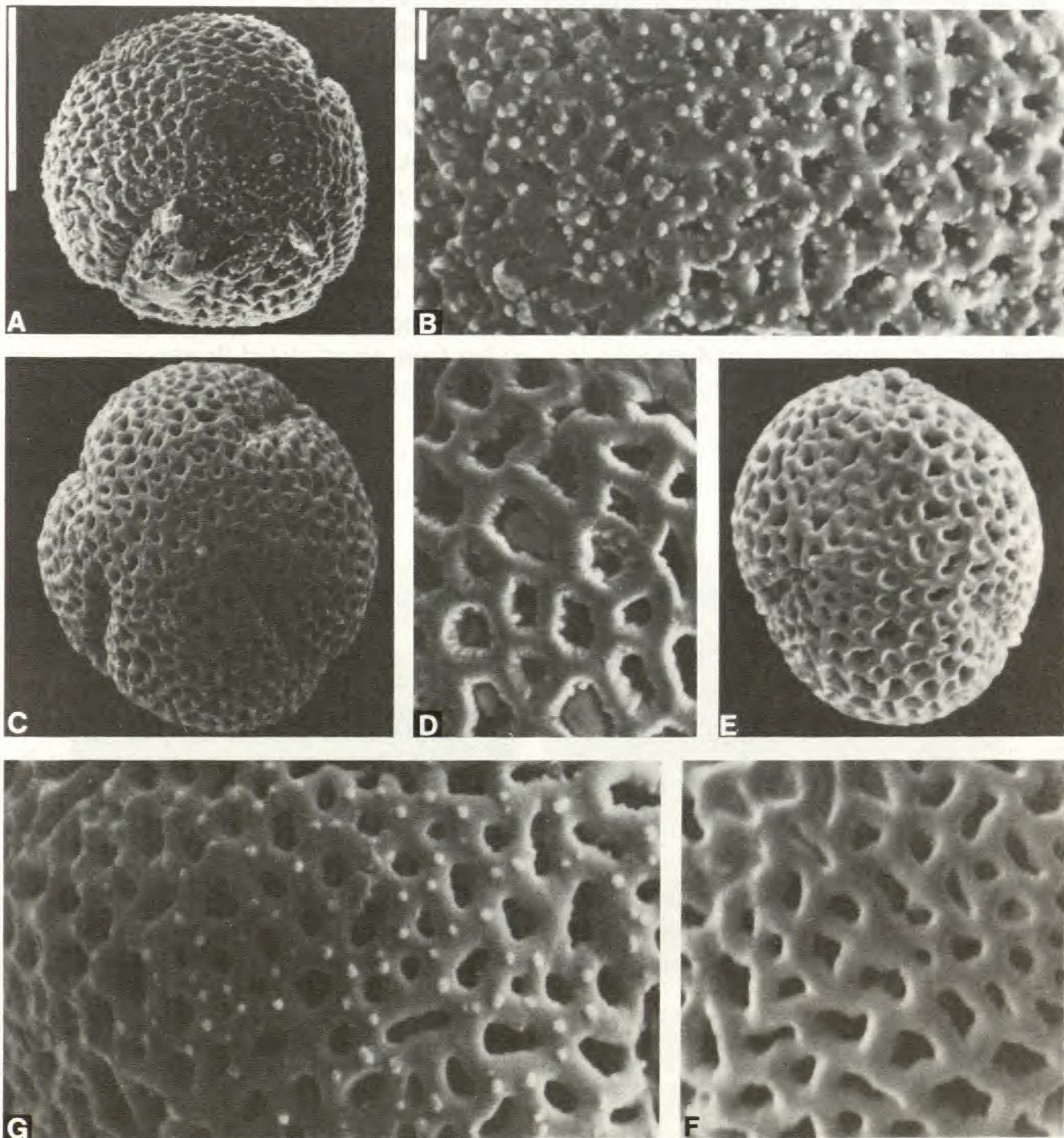


Fig. 16. — Pollen of A-D, *Payera coriacea* and E-G, *Schismatoclada viburnoides* : A-B, short-styled and C-D, long-styled morphs ; A, C, polar views ; B, D, details of mesocolpium ; E-F, long-styled and G, short-styled morph ; E, polar view ; F-G, details of mesocolpium. — Scale bars : $10\mu\text{m}$ (A = C = E) ; $1\mu\text{m}$ (B = D = F = G).

In all three genera, the exine is reticulate. SEM investigations reveal that pollen from short- and long-styled morphs exhibits differences in details of the exine. In pollen from short-styled flowers, the exine is invariably beset with suprategal verrucae, whereas pollen from long-styled flowers always has a smooth exine without suprategal verrucae (Fig. 15-16).

An identical situation was recently also noted for various other *Rubiaceae* (cf., for example, PUFF, 1988 and PUFF & ROBBRECHT, 1989) but, in addition, a dimorphism in the reticulum was reported (reticulum with a rather narrow mesh, i.e., exine finely reticulate, in short-styles, and with a wide mesh, i.e., exine coarsely reticulate, in long-styles). Such a reticulum dimorphism, however, is by no means obvious in any of the three investigated genera. If present at all, differences in the lumina of the exine are minimal. Differing lumen sizes in different parts of the grains, moreover, tend to obscure the situation. LEWIS (1965) had reported for *Schismatoclada psychotrioides* that pollen from short-styled flowers is "... coarsely reticulated", and that of long-styled flowers "... finely reticulated". Such marked differences in the reticulum pattern were not observed by us.

The present investigations indicate that differences in aperture number as recorded by LEWIS (1965 : Table 2) for *Schismatoclada psychotrioides* (pollen mostly 4-aperturate in short-

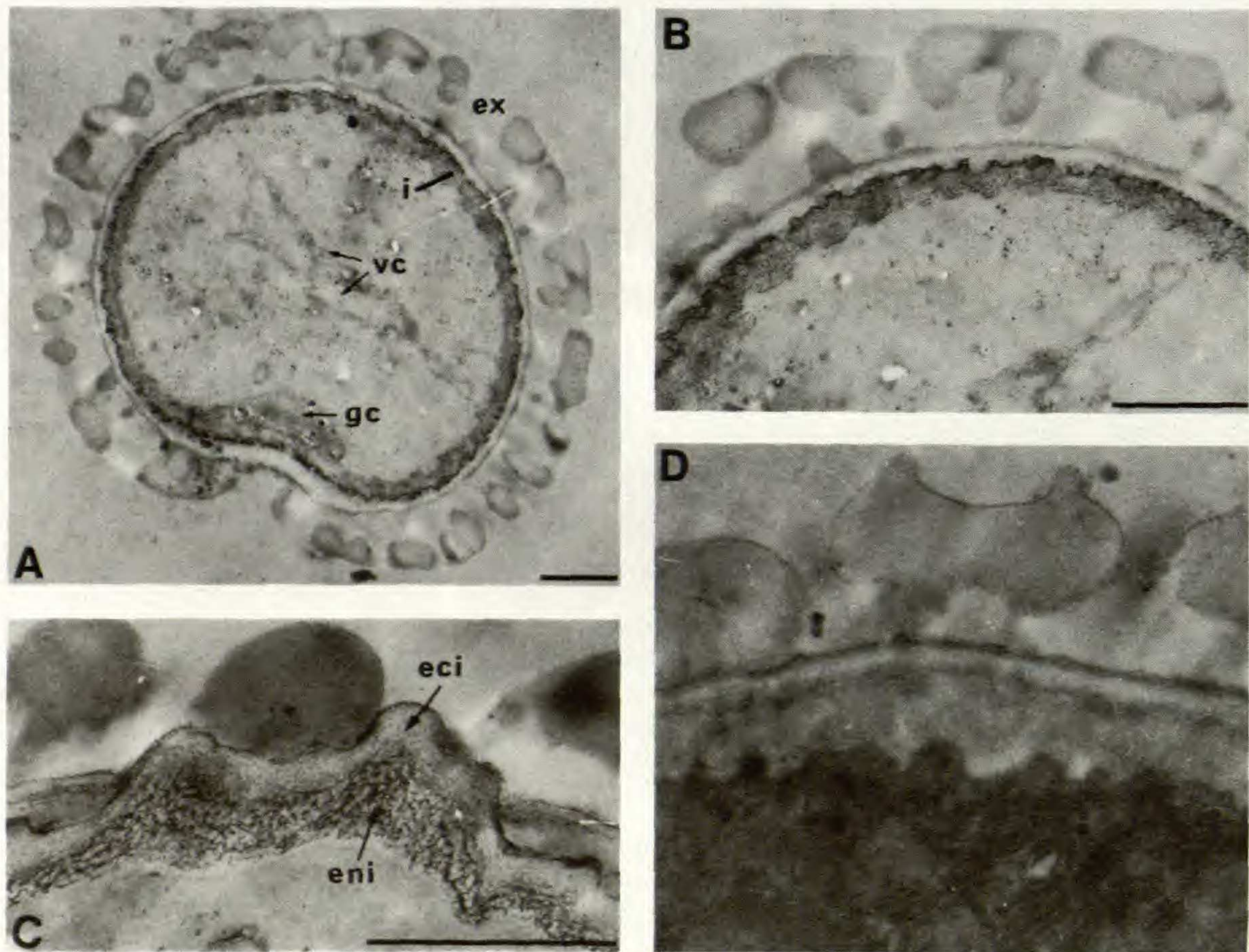


Fig. 17. — TEM-graphs of *Danais* pollen : A-B, *D. ligustrifolia*, long-styled morph; A, entire grain; B, detail of the wall; C-D, *D. rhamnifolia*, short-styled morph; C, detail of colpus region with ectexine element; D, portion of pollen grain wall with suprategal exine elements. — eni, endintine; eci, ectintine; ex, exine; gc, generative cell; i, intine; vc, vegetative cell. — A-C, Thiéry-test; D, contrasted with uranyl acetate and lead citrate. — Scale bars : 1 μ m (A; B; C = D).

and mostly 3-aperturate in long-styled flowers) may indeed be characteristic for the genus (cf. Table 3). In contrast, species of *Danais* might exhibit a heterostyly-linked dimorphism in pollen grain size. At least in a few taxa, pollen from long-styled flowers tends to be a little smaller than pollen from short-styled morphs (e.g. *D. fragrans* : 11-14 vs. 14-18 μm ; cf. Table 3). A similar difference in pollen grain size was also observed in the only *Payera* species, for which detailed data are available (*P. beondrokensis* : 24-28 vs. 28-30 μm ; cf. Table 3). Additional in-depth work, preferably on pollen material from long- and short-styled morphs of one and the same population, would be required to confirm how stable these differences are.

TEM investigations of the pollen wall structure of *Danais ligustrifolia* and *D. rhamnifolia* (Fig. 17) revealed that a massive, wavy intine is present (ca. 400 nm thick) which curves outward in the region of the colpi, where it bears small ectexine elements. A foot layer, ca. 80 nm thick, follows; above this is the exine (ca. 700 nm thick) with short columellae forming a reticulate tectum. TEM-graphs also very clearly show the suprategical verrucae on the exine of pollen from short-styled flowers (*D. rhamnifolia*; Fig. 17, D).

The mature pollen grains of *Danais* are binucleate. The pollen nuclear number in *Schismatoclada* and *Payera* could not be determined as no suitable preserved material was available.

VII. PHYTOCHEMICAL DATA

Relevant data about the genera in question are scarce. Nothing at all is known about *Payera*. Except for a brief note stating that three species of *Schismatoclada* are used as a febrifuge (BOITEAU, 1941), no further information is available on that genus.

There are, however, a few noteworthy reports on *Danais* : According to personal observations of one of us (C. P.) and also information given on herbarium labels, some *Danais* species (e.g. *D. cernua*, *D. fragrans* and *D. humblotii*) are characterized by the occurrence of an unpleasant foetid odour which is emitted when tissue is damaged. It is highly probable that, as in the genus *Paederia* (*Rubiaceae* tribe *Paederieae*), the presence of the iridoid glycoside paederoside is the cause for this (cf. TAKEDA et al., 1991 for details and further explanations). Unpleasant odour may be one of the reasons for the plants' usage in local folk medicine. It needs to be stressed, however, that foetid odour is not omnipresent in *Danais*. As observed in the field (C. P.), it is definitely absent in, for example, *D. volubilis*. Because of the generally poor documentation on herbarium labels, it is at present unknown how widespread its occurrence in *Danais* is. Foetid odour appears to be universally absent in both *Payera* and *Schismatoclada*; neither personal observations nor data on herbarium labels yielded any indication for their presence.

Moreover, the anthraquinones danain and danaidin are recorded for *Danais* (BOITEAU, 1941; HEGNAUER, 1973, 1990; see there for further references). Both are mostly found in the stems (bark) and roots.

In Madagascar, locals use the bark of *Danais* species as a febrifuge, and the roots against herpes.

VIII. CHOROLOGY (Fig. 18)

Except for *Danais*, the genera dealt with here are Malagasy endemics centred in the west Eastern Region (“East Malagasy Region”, “Région du vent”; HUMBERT, 1955*b*, 1965; KOEHLIN, 1972; WHITE, 1983).

Danais is more widespread. Its distribution range extends from Madagascar northwestward to the African mainland and eastwards to the Mascarene Islands (Fig. 18). The majority of *Danais* species, however, are Malagasy endemics.

Only one species, *D. xanthorrhoea*, is truly African (endemic to North East Tanzania). It is obviously closely allied to Malagasy taxa, namely to *D. rhamnifolia*. *D. xanthorrhoea* is largely confined to the Usambara and Uluguru Mts., two mountain ranges which are considerably older than the surrounding volcanic high East African mountains (cf. PÓCS, 1982). It thus seems that *Danais* may be yet another example for a genus exhibiting an “old” Madagascar-East Africa connection.

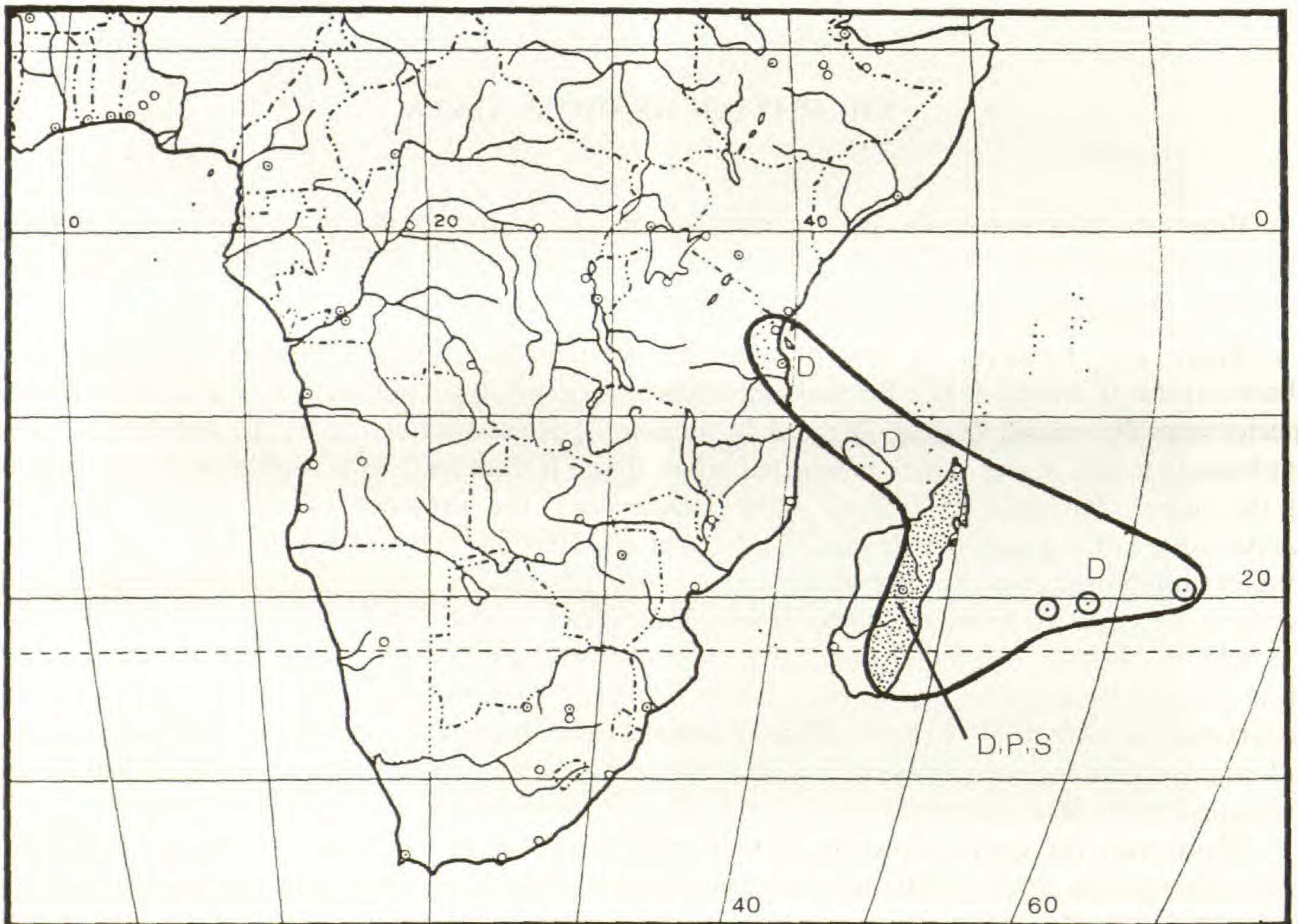


Fig. 18. — Distribution of the **Danais-Payera-Schismatoclada** complex. All three genera (D, P, S) occur in Madagascar, only *Danais* (D) is also found outside.

Another species, *D. humblotii*, extends from Madagascar to the Comoro Islands; the somewhat obscure species *D. comorensis* may be endemic to the Comoro Islands (see PUFF & BUCHNER, in press for comments).

Only three *Danais* species occur on the Mascarene Islands: *D. sulcata* is endemic to Mauritius and *D. corymbosa* to Rodriguez; the latter is likely to be extinct and has not been collected for more than 100 years (VERDCOURT, 1983, 1989). *D. fragrans*, the most widely distributed species, occurs in Mauritius, Réunion and Madagascar.

Taxa of *Danais* appear to be primarily rain-forest inhabitants. This is at least true for the majority of Malagasy taxa and the East African *D. xanthorrhoea*.

Like the other genera in question, *Danais* is largely confined to the East Malagasy Region. Within this Region, there is a clear ecological differentiation: *Danais coronata* (syn. *D. littoralis*), for example, is confined to the lowland rain forest region ("forêt orientale" *sensu* HUMBERT, 1965) and only occurs from the sea coast inland to an altitude of ca. 300 m. Other species, e.g. *D. aurantiaca*, primarily grow in "rain forest of medium elevation" (*sensu* RAUH, 1973). A number of taxa have a distribution range which is largely confined to the Central Plateau, where they are frequently found at the edge of evergreen forest remnants or in gallery forest (e.g. *D. hispida*).

While several Malagasy taxa of *Danais* have relatively wide distribution ranges within the East Region which may stretch from the North to the South Eastern tip of the island (e.g. *D. cernua*), other taxa are characterized by restricted ranges (e.g. *D. nigra*: only in the Northeast).

A few taxa (e.g. *D. verticillata*) are only known from the type collections made towards the end of the last century and only very few or even single collections from more recent times. It is suspected that such obviously rather rare species may meanwhile have become extinct since, in spite of intensive collecting activities in the last years (by, for example, the Missouri Botanic Garden), they have not been found again (see also PUFF & BUCHNER, in press).

Chorological data as detailed as for *Danais* are neither available for *Schismatoclada* nor for *Payera*. It, nevertheless, appears that the same general patterns apply. The only difference seems to be that both in *Payera* and *Schismatoclada* some species (e.g. *Payera coriacea*, *Schismatoclada marojejyensis*) also extend to — or are confined to — high mountain areas of Madagascar (afromontane vegetation).

IX. DISCUSSION

1. CHARACTERS BY WHICH *Danais*, *Schismatoclada* AND *Payera* CAN BE DISTINGUISHED (Table 4)

In Table 4, selected character states of *Danais*, *Schismatoclada* and *Payera* are listed, including those by which the genera can be distinguished.

An analysis of this table shows that characters often vary within the genera dealt with so that there is a certain overlap which makes a clear-cut distinction on the basis of a single character state impossible. If one, for example, looks at the character "calyx lobes" it transpires that long, narrow calyx lobes, although the typical situation for *Payera*, also do

TABLE 4 : Comparison of selected character states of **Danais**, **Schismatoclada** and **Payera** (incl. **Coursiana**).

Characters	<i>Danais</i>	<i>Schismatoclada</i>	<i>Payera</i> (incl. <i>Coursiana</i>)
<i>Growth form</i>	lianas or <i>climbing</i> shrubs	shrubs or small trees, never lianaceous	shrubs or small trees, never lianaceous
<i>Stipules</i>	small, entire (very seldom bifid or plurifimbriate, with laciniate margins, or connate)	often small, entire, \pm connate; sometimes plurifimbriate	often (very) large and with laciniate margins or multifimbriate
<i>Inflorescence</i> : — position	terminal (plus axillary); axillary (plus occasionally also terminal)	terminal	terminal
— shape	lax to congested	mostly \pm lax	often \pm congested
— subtended by involucre (enlarged bracts)	never	never	often yes
<i>Flowers</i> : — calyx lobes			
— size	small, seldom large	small to \pm large	often long, narrow; occasionally small
— indumentum	glabrous or hairy	glabrous	mostly hairy
— corolla			
— aestivation of lobes	valvate-reduplicate	valvate-reduplicate	valvate s. str.
— tube length	ca. 2-20 mm	ca. 5-30 mm	ca. 2-30 mm
— indumentum on outside	mostly absent; rarely hairy (long hairs)	generally absent (rarely outside of corolla lobes with long hairs)	adpressed hairs (“silvery hairy”)
— heterostyly	yes	yes	yes
<i>Fruits</i> : — shape	mostly \pm globose; never conspicuously elongated	mostly distinctly elongated; seldom globose	\pm globose; never conspicuously elongated
— size	ca. 2-15 mm in diam.	7-15 mm long	ca. 3-6 mm in diam.
— apex	never conspicuously beaked (Fig. 10, A-B)	beaked; beaks sometimes bilobed in dehisced fruits (Fig. 10, E-H)	beaked; beaks never distinctly bilobed in dehisced fruits (Fig. 10, I-K)
— dehiscence	loculicidal	septicidal	loculicidal
<i>Seeds</i> : — wing	\pm round to \pm asymmetrical conspicuous	elongated, \pm tripartite, conspicuous (Fig. 14, A)	\pm rectangular to \pm asymmetrical, inconspicuous, small (Fig. 14, B-E)
— size (incl. wing; diam. or greatest length)	ca. 0.6-6 mm	4-5 mm	0.5-2 mm
<i>Leaf anatomy</i>	multiple epidermis (Fig. 1, E) or epi- and hypodermis (Fig. 1, G)	“normal” epidermis (Fig. 2, C)	“normal” epidermis (Fig. 2, D) or epi- and hypodermis (Fig. 2, E)

occur in *Danais* but are uncommon in that genus. The presumably convergent developments make it necessary to use a combination of character states to characterize the genera.

The following comprehensive key to the genera demonstrates this :

1. Lianas or *climbing* shrubs; mature fruits never conspicuously beaked, always dehiscing loculicidally, mostly \pm globose, ca. 3-12 mm in diam.; inflorescences either essentially terminal or predominantly in the axils of foliage leaves *Danais*
- 1'. Shrubs or small trees, never strictly lianaceous; mature fruits beaked, dehiscing septi- or loculicidally, either elongated and ca. 7-15 mm long or \pm globose and ca. 3-6 mm in diam.; inflorescence essentially terminal.
2. Fruits always dehiscing septicidally, mostly distinctly elongated, never globose, ca. 7-15 \times 4-5 mm; beaks sometimes bilobed in dehisced fruits; seeds (including the wing) elongated and \pm narrowly ovate or elliptic, ca. 4 times as long as wide; aestivation of corolla lobes valvate-reuplicate *Schismatoclada*
- 2'. Fruits always dehiscing loculicidally, \pm globose, never conspicuously elongated, ca. 3-6 mm in diam., sometimes \pm ribbed; beaks never distinctly bilobed in dehisced fruits; seeds (including the wing) often \pm rectangular, only ca. 2-3 times as long as wide; aestivation of corolla lobes valvate (s. str.) *Payera*

2. NOTES ON THE TAXONOMIC POSITION AND RELATIONSHIPS OF THE **Danais-Schismatoclada-Payera** COMPLEX

The above detailed description of the character states of *Danais*, *Schismatoclada* and *Payera* leaves no doubt that the three genera form a closely related and apparently \pm isolated complex which does not seem to have obvious allies in Madagascar.

The tribal (and subfamilial) affiliation of this genus complex, however, is by no means unambiguous (see also III., Taxonomic History and Table 1) and still poses problems. ANDERSSON & PERSSON (1991), based on a cladistic analysis, provisionally transferred *Danais*, *Schismatoclada* and *Payera* (as *Coursiana*) to the *Hedyotideae*. According to the senior author (ANDERSSON, pers. comm.), however, the data set for the genera in question had been incomplete and possibly not fully reliable (because the data were primarily taken from the then available literature). It is, therefore, not so certain whether the cladistic analysis had yielded the same results, had the full data set been used that is now available. There are, in fact, arguments that could be brought forward against such a transfer to the *Hedyotideae* (see below).

The principal problem of the *Danais-Schismatoclada-Payera* complex is that its genera are characterized by a set of features which are (a) in part typical for the *Hedyotideae* (subfam. *Rubioideae*), (b) in part typical for alliances placed in the subfam. *Cinchonoideae* and (c) in part found in both subfamilies.

A few selected examples of this state of affairs are :

— Woody lianas (as in *Danais*) also occur in the *Cinchonoideae* (e.g. *Coptosapelta*; *Cinchoneae* s.l., or *Coptosapelteae sensu* ANDERSSON & PERSSON, 1991); in the *Hedyotideae*,

lianaceous taxa (e.g. *Hedyotis* spp.) are herbaceous (the tribe as such has predominantly herbaceous representatives).

— Raphides (as characteristic for *Danais* and allies) are typical for the *Hedyotideae* (and the subfam. *Rubioideae*), but they also occur in woody alliances of the *Cinchonoideae*, although they are less common.

— Foetid odour (i.e., the presence of the iridoid glycoside paederoside, see VII. Phytochemical Data) is recorded for various groups of the *Rubioideae* (including some genera of the *Hedyotideae*) but apparently absent in the *Cinchonoideae*.

— Both septi- and loculicidal capsules occur in *Hedyotideae* and *Cinchonoideae* (*Cinchoneae* s.l., etc.). Rather thick-walled, woody capsules as in *Danais* and allies are rather more common in the latter.

— Winged seeds (diverse in fine structure, size and shape of the wings) are very characteristic for many members of the *Cinchonoideae*. Their presence in *Danais* and allies has been one of the main arguments for an alliance with that subfamily and the *Cinchoneae* in particular. On the other hand, the opinion had been voiced that in a lianaceous genus like *Danais* winged seeds, advantageous for anemochorous dispersal, are merely an adaptation to its life form and can, therefore, not be interpreted as indicating a relationship to other alliances (BREMEKAMP's, 1966, argumentation). Exotesta cells of the *Cinchoneae* s.l. are characterized by the presence of reticulate thickenings of the inner tangential walls (BREMEKAMP, 1966; VERDCOURT, 1958), whereas conspicuous thickenings are lacking in the *Hedyotideae*. The kind of exotesta cells observed in *Danais* and allies (thickenings on the radial walls) fit neither group.

As a result of this situation, different authors subjectively suggested either a placement in the *Hedyotideae* (because they considered character state agreements with that tribe or with the *Rubioideae* in general more important), or a position in the *Cinchoneae* s.l. (because they stressed characters which the taxa have in common with the *Cinchonoideae* while, at the same time, discounting as unimportant features that indicate a link to the *Rubioideae*).

The conclusion is reached that in spite of the detailed data obtained in the course of the current study it, at present, is neither possible to clearly and objectively assign the genus complex in question to a tribe of the subfam. *Rubioideae* nor to place it in a tribe of the *Cinchonoideae*. — The logical consequence of this would be to establish a new tribe for this alliance, without assigning it to any of the subfamilies. We refrain from doing so and rather prefer to wait until such a time when more detailed, comparative data become available.

The case of the *Danais-Schismatoclada-Payera* complex appears to indicate that there is a systematic "grey zone" between the two subfamilies and the present study, once again, shows that the delimitation of the two subfamilies does not seem to be entirely clear-cut, a view already expressed by ROBBRECHT (1988).

ACKNOWLEDGEMENTS : We would like to thank Mr. J. GUÉHO (Mauritius Sugar Research Institute) and Dr. G. SCHATZ (Missouri Botanical Garden) for providing preserved material and colour slides, respectively. C. P. wishes to acknowledge support by the Fonds zur Förderung der Wissenschaftlichen Forschung (Project P8260-BIO).

LITERATURE CITED

- ANDERSSON, L. & PERSSON, C., 1991. — Circumscription of the tribe *Cinchoneae* (*Rubiaceae*) — a cladistic approach. *Pl. Syst. Evol.* 178 : 65-94.
- BAKER, J. G., 1883. — Contributions to the Flora of Madagascar. Part II. *Monopetalae*. *J. Linn. Soc. (Bot.)* 20 : 159-236.
- BAILLON, H., 1880. — *Histoire des plantes* 7. Hachette, Paris.
- BOITEAU, P., 1941. — Introduction à l'étude des plantes fébrifuges de la flore malgache. *Bull. Acad. Malg.* 24 : 1-17.
- BREMEKAMP, C. E. B., 1948. — On a species of *Danais* Commers. ex. Vent. occurring on the African continent. *Kew Bull.* 1948 : 188-190.
- BREMEKAMP, C. E. B., 1952. — The African species of *Oldenlandia* L. *sensu* Hiern et K. Schumann. *Verh. Koninkl. Ned. Akad. Wetensch., Afd. Natuurk., 2. Sect.* 18 : 1-297.
- BREMEKAMP, C. E. B., 1966. — Remarks on the position, the delimitation and the subdivision of the *Rubiaceae*. *Acta Bot. Neerl.* 15 : 1-33.
- CAVACO, A., 1964. — Contribution à l'étude des Rubiacées de Madagascar. I. Cinchonées. *Adansonia*, sér. 2, 4 : 185-195.
- CAVACO, A., 1965. — Contribution à l'étude des Rubiacées de Madagascar : *Danais* nouveaux. *Adansonia*, sér. 2, 6 : 439-442.
- CAVACO, A., (« 1965 ») 1966. — Les *Danais* (*Rubiaceae*) de Madagascar et des Comores. *Bull. Mus. natn. Hist. nat., Paris*, sér. 2, 37 : 717-723.
- CAVACO, A., 1967. — Synonymie et une espèce nouvelle dans le genre *Schismatoclada* (Rubiacées). *Adansonia*, sér. 2, 7 : 363-364.
- CAVACO, A., 1968a. — Contribution à l'étude des Cinchonées (Rubiacées) de Madagascar. *Adansonia*, sér. 2, 8 : 69-71.
- CAVACO, A., 1968b. — Note sur quelques Rubiacées de Madagascar et des Comores. *Adansonia*, sér. 2, 8 : 379-387.
- DRAKE DEL CASTILLO, M. E., (« 1897 ») 1898a. — Histoire naturelle des plantes. Tome IV. — Atlas. — IV (1) [45^e fasc.]. In : GRANDIDIER, A. (ed.), *Histoire physique, naturelle et politique de Madagascar*. Vol. 36. Imprimerie Nationale, Paris.
- DRAKE DEL CASTILLO, M. E., 1898b. — Note sur deux genres de Rubiacées des îles de l'Afrique orientale. *Bull. Soc. Bot. France* 45 : 344-356.
- DUBARD, M. & DOP, P., 1925. — Etude de quelques types nouveaux ou peu connus de Rubiacées de Madagascar. *J. Bot. (Morot)*, sér. 2, 3 : 1-31.
- ENDLICHER, S., 1838. — *Rubiaceae*. In : *Genera Plantarum secundum Ordines naturales disposita* [fasc. 6 & 7, 8] : 520-566. Beck, Vindobona.
- ERDTMAN, G., 1971. — *Pollen morphology and plant taxonomy. Angiosperms*. Corrected reprint of 1952 Edition. New York, Hafner.
- HEGNAUER, R., 1973. — *Chemotaxonomie der Pflanzen* 6. Birkhäuser, Basel, Stuttgart.
- HEGNAUER, R., 1990. — *Chemotaxonomie der Pflanzen* 9. Birkhäuser, Basel, Boston, Berlin.
- HOLMGREN, P. K., HOLMGREN, N. H. & BARNETT, L. C., 1990. — *Index Herbariorum*. Part I : The herbaria of the world. Ed. 8. New York Botanical Garden, Bronx, New York [Regnum Vegetabile vol. 120].
- HOMOLLE, A.-M., 1936. — *Danais* (Rubiacées) nouveaux de Madagascar, avec révision de la synonymie. *Notul. Syst. (Paris)* 5 (4) : 278-288.

- HOMOLLE, A.-M., 1939. — Rubiacées nouvelles de Madagascar. *Notul. Syst. (Paris)* 8 (1) : 26-32.
- HOMOLLE, A.-M., 1942. — Notes sur quelques plantes rares et mal représentées de la tribu des Cinchonées (Rubiacées). *Bull. Soc. Bot. France* 89 : 53-57.
- HOOKER, J. D., 1873. — Ordo LXXXIV. *Rubiaceae*. In : BENTHAM, G. & HOOKER, J. D. (ED.), *Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata defirmata*, 2 : 7-151. London, Reeve.
- HUMBERT, H., 1955a. — Une merveille de la nature à Madagascar. Première exploration botanique des massifs du Marojejy et ses satellites. *Mém. Inst. Sci. Mad.*, sér. B (Biol. Vég.), 6 : 1-210.
- HUMBERT, H., 1955b. — Les territoires phytogéographiques de Madagascar. In : Les divisions écologiques du monde. *Colloques Int. CNRS* 59 : 195-204. [also publ. in *Année biol.*, sér. 3, 31 : 439-448].
- HUMBERT, H., 1965. — Description des types de végétation. In : HUMBERT, H. & COURS DARNE, G. et al. (ed.), Notice explicative « Madagascar » : 49-75. *Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry*, hors sér. 6.
- KOECHLIN, J., 1972. — Flora and vegetation of Madagascar. In : BATTISTINI, R. & RICHARD-VINDARD, G. (ed.), *Biogeography and ecology in Madagascar (= Monogr. Biol. 21)* : 145-190. W. Junk, The Hague.
- LEWIS, W. H., 1965. — Cytopalynological study of African *Hedyotideae (Rubiaceae)*. *Ann. Missouri Bot. Gard.* 52 : 182-211.
- NAPP-ZINN, K., 1973. — Anatomie des Blattes. II. Blatt Anatomie der Angiospermen. A. Entwicklungsgeschichte und topographische Anatomie des Angiospermenblattes, 1. In : LINSBAUER, K. (ed.), *Handbuch der Pflanzenanatomie. Spezieller Teil*, ed. 2, 8 (2A, 1). Borntraeger, Berlin, Stuttgart.
- PETERSON, R. L., HERSEY, R. E. & BRISSON, J. D., 1978. — Embedding softened herbarium material in Spurr's resin for histological studies. *Stain Technol.* 53 : 1-9.
- PÓCS, T., 1982. — *The forest flora and vegetation of the old crystalline mountains of Tanzania and their importance for soil and water conservation*. Seminar/Workshop of Forest Conservation in Tanzania, Tanga; mimeogr., 5 pp.
- PUFF, C., 1988. — Observations on *Carphalea* Juss. (*Rubiaceae-Hedyotideae*), with particular reference to the Madagascan taxa and its taxonomic position. *Bull. Jard. Bot. Nat. Belg.* 58 : 272-323.
- PUFF, C. & BUCHNER, R., in press. — Revision of *Danais* Vent. (*Rubiaceae*) in Madagascar and the Comores. *Adansonia*.
- PUFF, C. & IGRSHEIM, A., 1991. — The flowers of *Paederia* L. (*Rubiaceae-Paederieae*). In : PUFF, C. (ed.), *The genus Paederia L. (Rubiaceae-Paederieae) : a multidisciplinary study*. *Opera Bot. Belg.* 3 : 55-75.
- PUFF, C., IGRSHEIM, A. & ROHRHOFER, U., 1993. — *Pseudomussaenda* and *Schizomussaenda (Rubiaceae)* : close allies of *Mussaenda*. *Bull. Jard. Bot. Nat. Belg.* 62 : 35-68.
- PUFF, C. & ROBBRECHT, E., 1989. — A survey of the *Knoxieae (Rubiaceae-Antirheoideae)*. *Bot. Jahrb. Syst.* 110 : 511-558.
- RAUH, W., 1973. — Über die Zonierung und Differenzierung der Vegetation Madagaskars. *Trop. Subtrop. Pflanzenwelt* 1 : 1-146.
- ROBBRECHT, E., 1988. — Tropical woody *Rubiaceae*. *Opera Bot. Belg.* 1 : 1-271.
- SCHUMANN, K., 1891. — *Rubiaceae*. In : ENGLER, A. & PRANTL, K. (ed.), *Die natürlichen Pflanzenfamilien* 4 (4) : 1-156. Engelmann, Leipzig.
- SPURR, A. R., 1969. — A low-viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* 26 : 31-43.
- TAKEDA, Y., PUFF, C., KONDOH, Y. & YOSHIOKA, Y., 1991. — Analysis of iridoid glycosides of *Paederia* L. species (*Rubiaceae-Paederieae*) by gaschromatography and gaschromatography-mass spectrometry. In : PUFF, C. (ed.), *The genus Paederia L. (Rubiaceae-Paederieae) : a multidisciplinary study*. *Opera Bot. Belg.* 3 : 153-158.

- THIÉRY, J.-P., 1967. — Mise en évidence des polysaccharides sur coupes fines en microscopie électronique. *J. Microscopie* 6 : 987-1018.
- VERDCOURT, B., 1958. — Remarks on the classification of the *Rubiaceae*. *Bull. Jard. Bot. Etat Brux.* 28 : 209-281.
- VERDCOURT, B., 1976. — *Rubiaceae* (part 1). In : POLHILL, R. M. (ed.), *Flora of Tropical East Africa* : 1-414. Agents for Oversea Governments and Admin., London.
- VERDCOURT, B., 1983. — Notes on Mascarene *Rubiaceae*. *Kew Bull.* 37 : 521-574.
- VERDCOURT, B., 1989. — 108. Rubiacées. In : BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (ed.), *Flore des Mascareignes* : 1-135. Sugar Ind. Res. Inst., Mauritius.
- VOGEL, S., 1954. — Blütenbiologische Typen als Elemente der Sippengliederung. *Bot. Stud.* 1 : 1-338.
- WEBER, M., 1989. — Thiéry-test in combination with an uranyl acetate/lead citrate staining. *Stain Technol.* 64 : 147-149.
- WEBERLING, F., 1977. — Beiträge zur Morphologie der Rubiaceen-Infloreszenzen. *Ber. Deutsch. Bot. Ges.* 90 : 191-209.
- WHITE, F., 1983. — *The vegetation of Africa*. Natural Resources Research 20 : 1-356. UNESCO, Paris.
- WILKINSON, H. P., 1979. — The plant surface (mainly leaf). In : METCALFE, C. R. & CHALK, L. (ed.), *Anatomy of the Dicotyledons*. Ed. 2. Vol. 1 : Systematic anatomy of the leaf and stem, with a brief history of the subject : 97-165. Clarendon Press, Oxford.
- WODEHOUSE, R. P., 1935. — *Pollen grains*. McGraw Hill Book Company, New York, London.

APPENDIX

TAXA OF *PAYERA* AND *SCHISMATOCLADA* ACCEPTED IN THE PRESENT ARTICLE (INCLUDING NECESSARY NEW COMBINATIONS AND TRANSFERS)

PAYERA Baillon

- Bull. Mens. Soc. Linn. Paris 1 : 178 (1878); Hist. Pl. 4 : 458 (1880); K. SCHUM. in ENGLER & PRANTL, Natürl. Pflanzenfam. 4, 4 : 31 (1891), *nom. cons.* — Typus generis : *Payera conspicua* Baillon.
- *Coursiana* HOMOLLE [Bull. Soc. Bot. France 89 : 57 (1942); without specification of type or type species] ex CAVACO, *Adansonia*, sér. 2, 8 : 71 (1968). — Typus generis (*et species sola*) : *Coursiana homolleana* Cavaco [see *Payera homolleana*, below].

Payera conspicua Baillon

- Bull. Mens. Soc. Linn. Paris 1 : 179 (1878); DRAKE in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : *tab.* 450 (1898).

TYPE : *Lastelle s.n.*, Madagascar, without locality (holo-, P!).

OTHER COLLECTION SEEN : "Central Madagascar", *Baron* 2578 (K).

SPECIES OF *Payera* ORIGINALLY DESCRIBED UNDER *Coursiana*, *Danais* OR *Schismatoclada*
(NEW COMBINATIONS)

Payera bakeriana (Homolle) Buchner & Puff, *comb. nov.*

— *Danais bakeriana* HOMOLLE, Notul. Syst. (Paris) 5 : 281 (1936); BOITEAU, Bull. Acad. Malg. 24 : 12 (1941).

TYPES : *Baron 2937*, Madagascar, "Central Madagascar" (lecto-, P!, selected here; isolecto-, K!); *Baron 3444* (syn-, BM!, K!, P!).

OTHER COLLECTIONS SEEN : *Baron 4452, 5017* (both K); *Capuron SF 22640* (P); *Fosberg 52346* (MO); *Jacquemin 135-J* (P).

Payera beondrokensis (Humbert) Buchner & Puff, *comb. nov.*

— *Schismatoclada beondrokensis* HUMBERT, Mém. Inst. Sci. Madag., sér. B, 6 : 140 & fig. 13, 5-9 (1955); CAVACO, *Adansonia*, sér. 2, 4 : 191 (1964).

— *Danais beondrokensis* (HUMBERT) LEROY [noted on herbarium sheet].

TYPE : *Humbert 23487*, Madagascar, Beondroka summit (holo-, P!).

NOTE : apparently very close to the following species but differing in stipule structure and leaf margin indumentum.

Payera coriacea (Humbert) Buchner & Puff, *comb. nov.*

— *Schismatoclada coriacea* HUMBERT, Mém. Inst. Sci. Madag., sér. B, 6 : 139 & fig. 13, 1-4 (1955); CAVACO, *Adansonia*, sér. 2, 4 : 191 (1964).

TYPE : *Humbert 22762*, Madagascar, Marojejy massif (holo-, P!).

OTHER COLLECTIONS SEEN : *Cours 3485* (P); *Humbert & Cours 23823* (P); *Humbert & Saboureau 31884* (P); MILLER & Lowry 4151 (K, MO).

Payera decaryi (Homolle) Buchner & Puff, *comb. nov.*

— *Danais decaryi* HOMOLLE, Notul. Syst. (Paris) 5 : 282 (1936); BOITEAU, Bull. Acad. Malg. 24 : 13 (1941).

TYPES : *Decary 10349*, Madagascar, Fort Dauphin Distr. (lecto-, P!, selected here); *Decary 10382, 10839* (syn-, P!).

OTHER COLLECTIONS SEEN : *Homolle D1* (P); *Puff 800809-1/1* (WU); *Réserves naturelles Mad RN 2633* (P); *Schatz & Nicoll 1236* (K, MO) [also BR, C, DSM, EA, ERE, G, GH, LE, NY, P, PRE, PTBG, S, SRGH, TAN, US, WAG].

Payera homolleana (Cavaco) Buchner & Puff, *comb. nov.*

- *Coursiana homolleana* CAVACO, *Adansonia*, sér. 2, 8 : 71 (1968).
- *Danais ambatondrazakensis* LEROY [noted on herbarium sheets].

TYPE : *Cours 1156*, Madagascar, Sahalampy (Onibé), Ambatodrazaka Distr. (holo-, P!).

OTHER COLLECTIONS SEEN : *Baron 2616* (P-fragment); *Capuron SF 23720* (P); *Cours 2756* (P), *4657* (P); *Humbert 5773* (P).

NOTE : The collections vary in their indumentum from densely hairy (type) to rather sparsely (*Humbert 5773*).

Payera madagascariensis (Cavaco) Buchner & Puff, *comb. nov.*

- *Danais madagascariensis* CAVACO, *Adansonia*, sér. 2, 5 : 441 & pl. 1, 1-10 (1965).
- *Danais ampasimenensis* LEROY, *nom. in herb.*

TYPE : *Humbert 20577*, Madagascar, Manampanihy valley, around Ampasimena (holo-, P!).

NOTE : The sheet bears a revision label saying “*Payera madagascariensis* Cavaco. Det. CAVACO, 1967” but gives no indication whatsoever that it is actually the holotype of his own *Danais madagascariensis* Cavaco [CAVACO, by the way, has never published this; in none of his articles he dealt with *Payera*]. LEROY, obviously not realizing that he had in hand the type of *Danais madagascariensis* (in fact, “*Danais*” is not written anywhere on the label or on the sheet), apparently intended to transfer “*Payera madagascariensis* Cavaco” back to *Danais* and meant (on a revision label dated 22-3-1975) “*Danais ampasimenensis*” to be a *nom. nov.* because he was aware that the name *Danais madagascariensis* already existed.

Only known from the type.

Payera mandrarensis (Homolle ex Cavaco) Buchner & Puff, *comb. nov.*

- *Danais mandrarensis* HOMOLLE ex CAVACO, *Bull. Mus. Hist. Nat. Paris*, sér. 2, 37 : 718 (1966).

TYPE : *Humbert 14039*, Madagascar, mts. between Andohahela and Elakelaka, betw. Imonty and Tsiotsilo hill, Mananara basin, tributary of Mandrare R. (holo-, P!).

Only known from the type.

IMPORTANT NOTE : The above list of new combinations is possibly incomplete. We suspect that a few species which at present are still included in *Schismatoclada* might need to be transferred to *Payera*. — See below (“Additional taxa described under *Schismatoclada*”) for details.

NEW SPECIES OF *Payera*

Payera glabrifolia Leroy ex Buchner & Puff, *sp. nov.* — Fig. 4, E.

— *P. glabrifolia* LEROY, *nom. nud. in herb.*

P. homolleana affinis sed foliis glabris differt.

TYPE : *Cours 4930*, Madagascar, "Itinéraire de Didy à Brickaville", without date (holo-, P!).

Presumably a shrub, length of the terete stems unknown; young parts with adpressed greyish hairs. Leaves decussate; leaf-blades \pm membranous, lanceolate, gradually narrowed to the apex and to the base, 130-150 \times 15-30 mm, glabrous above and below; petioles to ca. 10 mm long, glabrous; stipules foliaceous, lanceolate, 15-24 \times 3-5 mm, margins lacinate, pubescent (especially on the margins). Inflorescences terminal, many-flowered, capituliform, comprised of much congested cymes, ca. 30 mm in diam.; subtended by leaf-like bracts. Flowers 5-merous, heterodistylous; calyx lobes (linear-)lanceolate, ca. 7-8 mm long, erect, pubescent. Corolla colour unknown; tube ca. 2-3 mm long, narrowly funnel-shaped to \pm cylindrical, ca. 0.6-0.7 mm wide at the base and ca. 1.2-1.4 mm wide above in short-styled flowers, densely covered with adpressed greyish hairs on the outside; lobes oblong, ca. 5.5 \times 0.8 mm, hairy outside. Stamens exerted for ca. 4-5 mm; anthers ca. 2 mm long; filiform style plus stigmas shorter than the corolla tube (short-styled flowers; long-styled flowers not seen). Ovary subglobose, ca. 1 mm long, pubescent. Mature fruits and seeds unknown.

Only known from the type.

Payera marojejyensis Buchner & Puff, *sp. nov.*

— *Danais marojejyensis* LEROY, *nom. nud. in herb.*

P. coriacea affinis sed foliis pubescentibus differt.

TYPE : *Humbert & Cours 23822*, Madagascar, Marojejy massif, à l'ouest de la haute Manantenina, affluent de la Lokoho, 26 Mars-2 Avril 1949 (holo-, P!).

Shrublet, much-branched, ca. 0.5 m tall; young part densely covered with rusty- to golden-brown hairs. Leaves decussate, usually clustered at the apex of branchlets; leaf-blades coriaceous, ovate or ovate-elliptic, 20-45 \times 12-25 mm, acute to \pm rounded at the apex, rounded to \pm cuneate at the base, with rusty- to golden-brown hairs above and below, but hairs denser and longer below, venation conspicuous above and below (veins raised below, but sunk above); blades discolourous (dark brown above, rusty- to golden-brown below); petioles to ca. 3-5 mm long, pubescent; stipules \pm rounded, 4-6 \times 4-8 mm, margins lacinate, with

several to \pm many appendages ca. 1-2 mm long, pubescent. Inflorescences terminal, several — to \pm many — flowered, comprised of quite condensed cymes, ca. 10-20 mm in diam.; inflorescence axes pubescent, pedicels somewhat elongated (to ca. 3 mm) and becoming glabrescent in fruit. Open flowers unknown. Calyx lobes of buds linear-lanceolate, 4-6 mm long, erect, pubescent; lobes spreading and \pm equally long after anthesis, mostly broken off and no longer present in fully mature fruits. Ovary (of buds and after anthesis) subglobose, ca. 1 mm in diam., pubescent. Fruits capsular, loculicidal, with a distinct beak, subglobose, ca. 5.5 mm in diam.; glabrous when fully mature. Seeds dark-brown, 1.6-2 mm in diam., with an irregularly lacerate, somewhat elongated, \pm tripartite wing.

OTHER COLLECTIONS SEEN : *Cours 3492, Humbert 22705* (both P).

NOTE : Although clearly related to *P. coriacea* and its close ally *P. beondrokensis*, the new species is very easily recognized by its pubescent leaves with their prominent venation pattern. It seems very odd that HUMBERT (1955a), when dealing with the *Rubiaceae* collected in the Marojejy massif during his 7th expedition to Madagascar (1948-49), did nowhere cite the three known collections of *P. marojejyensis* (all of which are from the \pm same locality).

SCHISMATOCLADA Baker

J. Linn. Soc. (Bot.) 20 : 159 (1883); BOITEAU, Bull. Acad. Malg. 24 : 14 (1941). — TYPUS GENERIS : *Schismatoclada psychotrioides* Baker.

SPECIES WHOSE IDENTITY HAS BEEN CONFIRMED

Schismatoclada citrifolia (Lamarck ex Poir.) Homolle

Notul. Syst. (Paris) 8 : 28 (1939); CAVACO, *Adansonia*, sér. 2, 4 : 188 & fig. 2, 1-2 (1964) & *Adansonia*, sér. 2, 7 : 363 (1967).

— *Mussaenda citrifolia* LAMARCK ex POIR., *Encycl. Méth.* 4 : 393 (1797).

— *Schismatoclada rupestris* HOMOLLE, Notul. Syst. (Paris) 8 : 31 (1939); CAVACO, *Adansonia*, sér. 2, 4 : 189 & fig. 2, 8-9 (1964). Type : *Humbert 12218*, Madagascar, Ivakoany massif (lecto-, P!; CAVACO, 1964).

TYPE : *Herb. Lamarck nr. 60*, Madagascar (holo-, P).

OTHER COLLECTIONS SEEN : *Decary 10444* (K) [also P].

Schismatoclada concinna Baker

J. Linn. Soc. (Bot.) 21 : 407 (1885); BOITEAU, Bull. Acad. Malg. 24 : 16 (1941); CAVACO, *Adansonia*, sér. 2, 4 : 186 (1964).

TYPE : *Baron s.n.*, Madagascar, without locality (holo-, K!; iso-, BM!, P).

OTHER COLLECTIONS SEEN : *Baron 376, 4460* (both P); *Humbert 24651* (P).

Schismatoclada marojejyensis Humbert

Mém. Inst. Sci. Madag., sér. B, 6 : 142 & fig. 13, 10-14 (1955); CAVACO, Adansonia, sér. 2, 4 : 191 (1964).

TYPE : *Humbert 23697*, Madagascar, Marojejy massif (holo-, P).

OTHER COLLECTIONS SEEN : *Miller & Lowry 4140* (K) [also MO].

Schismatoclada psychotrioides Baker

J. Linn. Soc. (Bot.) 20 : 160 & pl. 24A, 1-7 (1883); HOMOLLE, Notul. Syst. (Paris) 5 : 32 (1939); BOITEAU, Bull. Acad. Malg. 24 : 15 (1941); CAVACO, Adansonia, sér. 2, 4 : 186 (1964).

— *Schismatoclada tricholarynx* BAKER, J. Linn. Soc. (Bot.) 22 : 480 (1887); BOITEAU, Bull. Acad. Malg. 24 : 15 (1941). Type : *Baron 3632*, Madagascar, without locality (holo-, K!).

TYPES : *Baron 1320*, Madagascar, "forests of the province of Imerina" [fruits] (syn-, K!), *1769* [flowers] (lecto-, K!; isolecto-, P; CAVACO, 1964).

OTHER COLLECTIONS SEEN (selection) : *Gentry 11856* (K, MO), *HILDEBRANDT 3898* (BM, M, W, WU), *Schatz et al. 1376* (BR, MO).

Schismatoclada purpurea Homolle

Notul. Syst. (Paris) 8 : 31 (1939); CAVACO, Adansonia, sér. 2, 4 : 189 & fig. 1, 2-3 (1964).

TYPE : *Perrier de la Bâthie 15355*, Madagascar, massif du Tsaratanana (holo-, P!).

Schismatoclada thouarsiana (Baillon) Homolle

Notul. Syst. (Paris) 8 : 32 (1939); CAVACO, Adansonia, sér. 2, 4 : 191 (1964) & Adansonia, sér. 2, 7 : 364 (1967).

— *Mussaenda thouarsiana* BAILLON, Adansonia 12 : 295 (1879).

TYPE : *du Petit-Thouars s.n.*, Madagascar, without locality (holo-, P).

OTHER COLLECTIONS SEEN : *Schatz et al. 1923* (K) [also MO].

Schismatoclada viburnoides Baker

J. Linn. Soc. (Bot.) 21 : 407 (1885); DRAKE in GRANDIDIER, Hist. Phys. Madagascar 36 [Hist. Nat. Pl. 6] : tab. 455 (1898); BOITEAU, Bull. Acad. Malg. 24 : 16 (1941); HUMBERT, Mém. Inst. Sci. Madag., sér. B, 6 : 143 (1955); CAVACO, Adansonia, sér. 2, 4 : 186 (1964).

TYPE : *Baron 3220*, Madagascar, without locality (holo-, K!; iso-, P).

OTHERS COLLECTIONS SEEN : *Miller & Lowry 4121* (K) [also MO].

ADDITIONAL TAXA DESCRIBED UNDER **Schismatoclada**

We have not seen the type specimens of the taxa listed below. It is not entirely certain from the descriptions and/or illustrations whether all species are really correctly placed in *Schismatoclada*.

As references to original publications, types, synonyms, etc., on these taxa are given in CAVACO (1964, 1967, 1968a), this information is not repeated here.

Schismatoclada aurantiaca Homolle (1939). — *S. mandrarensis* HOMOLLE (1939) [CAVACO, 1964].

Schismatoclada aurea Homolle (1939)

Schismatoclada bracteata Homolle ex Cavaco (1964)

Schismatoclada coursiana Cavaco (1968)

Schismatoclada farahimpensis Homolle (1939)

Schismatoclada homolleae ["*homollei*"] Boiteau (1942)

Schismatoclada humbertiana Homolle (1939)

Schismatoclada longistipula Cavaco (1964)

Schismatoclada lutea Homolle (1939)

Schismatoclada pubescens Homolle (1939)

Schismatoclada rubra Homolle (1939)

var. **brevicalyx** (Humbert) Cavaco (1967). — *S. rupestris* HOMOLLE var. *brevicalyx* HUMBERT (1955)

Schismatoclada villiflora Homolle ex Cavaco (1964)

DANAIS

See PUFF & BUCHNER (in press) for taxa currently recognized in *Danais*.

Species originally described under *Danais* that are to be excluded from the genus : see the list of *Payera* species (above) and the following section.

SPECIES TO BE EXCLUDED FROM THE DANAIS-SCHISMATOCLADA-PAYERA COMPLEX

The following two species are excluded from the *Danais-Schismatoclada-Payera* complex primarily because they have unwinged seeds :

Danais aptera Homolle

Notul. Syst. (Paris) 5 : 279 (1936); BOITEAU, Bull. Acad. Malg. 24 : 6 (1941).

TYPE : *Chapelier s.n.*, Madagascar, "E Coast", without locality (holo-, P!; iso-, P!).

The species is a liana with solitary or, less commonly, fascicled long-pedicellate axillary fruits (no flowers are present in material studied). The fruits, sometimes also on older stem parts (CAVACO, 1966 : “inflorescences cauliflores”), do remind of *Danais* in both their round shape and in their loculicidal dehiscence, but the small \pm cylindrical seeds show no sign at all of a wing. The seeds are attached to the placenta by their short axis.

Danais ? baccata Homolle

Notul. Syst. (Paris) 5 : 280 (1936); BOITEAU, Bull. Acad. Malg. 24 : 14 (1941).

TYPE : *Perrier de la Bâthie* 12663, Madagascar, [E; alluvions des bords de l'] Itomampy R. (holo-, P!).

The species is shrubby and has both terminal and axillary inflorescences which are often 3-flowered (sometimes to 5-flowered, occasionally only uniflorous). The fruits, which appear to be \pm fleshy at first, dehisce loculicidally at maturity. Dehisced fruits reveal the presence of a thick, sclerenchymatic endocarp. As in the previous species, the fruits — although showing a basic similarity to *Danais* — release small, \pm cylindrical to \pm ellipsoidal wingless seeds.

Little can at present be said about the generic alliances of the two species except that, on account of their similar seeds, they might belong to one and the same genus. Whether this would be a new or an existing genus must remain unanswered because, firstly, our state of knowledge of Malagasy *Rubiaceae* in general is rather poor and because, secondly, the available material of the two species (only the collections cited above have been seen) is hardly sufficient for a thorough analysis of their character states and any conclusions to be drawn.