Pl. Syst. Evol. 196: 1–17 (1995)

Plant Systematics and Evolution

Ovary, seed and fruit of *Rutidea* (*Rubiaceae, Pavetteae*)

P. De Block

Received June 20, 1994; in revised version September 16, 1994

Key words: *Rubiaceae, Pavetteae, Rutidea, Nichallea.* – Ovary, incomplete septum, placentation, obturator, campylotropous ovule, fruit, seed development, rumination.

Abstract: The ovary of *Rutidea* is bicarpellate and incompletely bilocular (septum between locules not continuous). A solitary campylotropous ovule, ascending from a basal placenta, occurs in each locule. Based on their orientation and degree of curving, three ovule types are distinguished. As a consequence of the abortion of one ovule, the drupaceous fruits are one-seeded. The incomplete septum allows the spherical seed to fill out the entire interior of the fruit. The seeds are deeply ruminate (*Spigelia* type). They grow very fast, producing folds and undulations (ruminations) which invade and totally occupy the second locule, almost enveloping the aborted ovule. Comparisons with other *Rubiaceae* (especially *Pavetteae*), show that hemianatropy and campylotropy occur more often in the *Rubiaceae* than hitherto accepted. The study corroborates the close affinity between *Rutidea* and *Nichallea.*

Rutidea is a tropical African genus of about 22 species (Bridson 1978) belonging to the tribe *Pavetteae* of *Rubiaceae* subfam. *Ixoroideae* (Bridson & Robbrecht 1985, Robbrecht & Puff 1986, Robbrecht 1988). The genus is easily recognized by having an incompletely bilocular ovary with two basal ovules (described as being amphitropous in some older literature, e.g., Hooker 1873, Hiern 1877). Furthermore, it is characterized by unilocular fruits with a solitary, spherical, deeply ruminate seed (there is abortion of one of the ovules). Within the tribe *Pavetteae*, only the monospecific African genus *Nichallea* approaches *Rutidea* in all these features.

The aim of the present study is to document in detail the unusual structure of the ovary, the development of the fruit and seed, and the rumination process, and to relate the findings with the situation in other genera of the tribe *Pavetteae.*

Material and methods

The present study is based on the investigation of samples preserved in FPA or 70% ethanol from the herbaria BR, WAG, and WU. The findings were corroborated by studying dried herbarium specimens of BR. Illustrations were prepared from preserved material of the following collections:

Ixora burundiensis Bridson: Rwanda, Troupin 11196 (BR) (Fig. 4 B). – *Nichallea* *soyauxii* (Hiern) Bridson: Ivory Coast, De Koning 5387 (WAG) (Fig. 4 A). – *Pavetta oliveriana* Hiern: Ethiopia, Puff 821213-1/1 (WU) (Fig. 4 C). – *Rutidea fuscescens* Hiern subsp. *fuscescens*: Zaire, Malaisse 12556 (BR) (Fig. 2 B, D–F). – *R. fuscescens* Hiern subsp. *bracteata* Bridson: Rwanda, Troupin 9699 (Figs. 1 B, C; 2 C) and Troupin 10525 (BR) (Fig. 2 A). – *R. insculpta* Mildbr. ex Bridson: Zaire, J. Louis 13335 (BR) (Fig. 1 D).–*R. smithii* Hiern subsp. *submontana* (K. Krause) Bridson: Uganda; Puff 830716-1/11 (WU) (Figs. 5 E–G, 6 A, C). – *Rutidea* spec.: Sierra Leone, Puff 810719-1/2 (WU) (Figs. 1 A, 5 A–D, H, 6 B, D).

The methods for microtome sectioning and SEM-investigations follow those described by Igersheim (1993 a). In the following text, taxa will be referred to their position within the *Rubiaceae* by the mnemonic abbreviations for the tribe to which they belong, as given by Robbrecht (1988, 1993).

Results

General floral characteristics. *Rutidea* has 4- and 5-, or sometimes 6-merous flowers. The salver-shaped, usually white or cream corollas, with reflexed or spreading lobes are relatively small (seldom longer than 2 cm). The calyces are shorter than the corolla tubes and are comprised of a short basal tubular part and well developed free lobes. The stamens have short filaments and are attached to the throat of the corolla tube. The anthers are fully or sometimes partly exserted. The ovaries are crowned by fleshy, annular, glabrous disks, which surround the base of the styles. The upper part of the styles and the fused stigmatic areas are exserted and serve as pollen presenting organs (a study on the unusual and apparently highly specialized secondary pollen presentation in the genus is under preparation).

Flowering specimens of *Rutidea* are easily distinguished from those of other *Pavetteae*, because the latter usually have much larger flowers with narrowly cylindrical corolla tubes (up to 6 cm long in African *Ixora* and up to 15 cm in *Leptactina*) and much shorter corolla lobes. Flowers of the *Pavetteae* are mostly 5-merous, although 4-mery is characteristic for some genera (e.g., *Ixora* and *Pavetta*). *Rutidea* is the only genus with both 4- and 5-merous species (sect. *Tetramera* and sect. *Rutidea*, respectively).

Ovary structure and placentation. The ovary of *Rutidea* is bicarpellate and incompletely bilocular. There is one ovule per carpel. Although rare, there are also anomalous ovaries with three (incomplete) locules (see below for details).

The ovary must be described as incompletely bilocular because the septum between the locules is not a continuous structure (Fig. 2 B, D–F). The massive and thick "basal" part of the septum is not in direct contact with the "apical" septum portions. The latter is only present at the periphery of the ovarian cavity as a ridge-like outgrowth (Fig. 2 B), leaving the centre of the ovary free and the two locules continuous with each other. However, the two septal parts can be in contact via loose cell rows, giving the septum a continuous appearance (in ovaries with ovules of ovule type I; see below).

At anthesis, the ovary wall shows a differentiation into three tissue zones, namely

(i) the ovary epidermis, comprised of one layer of rectangular cells, covered with a thick cuticle (the later exocarp),

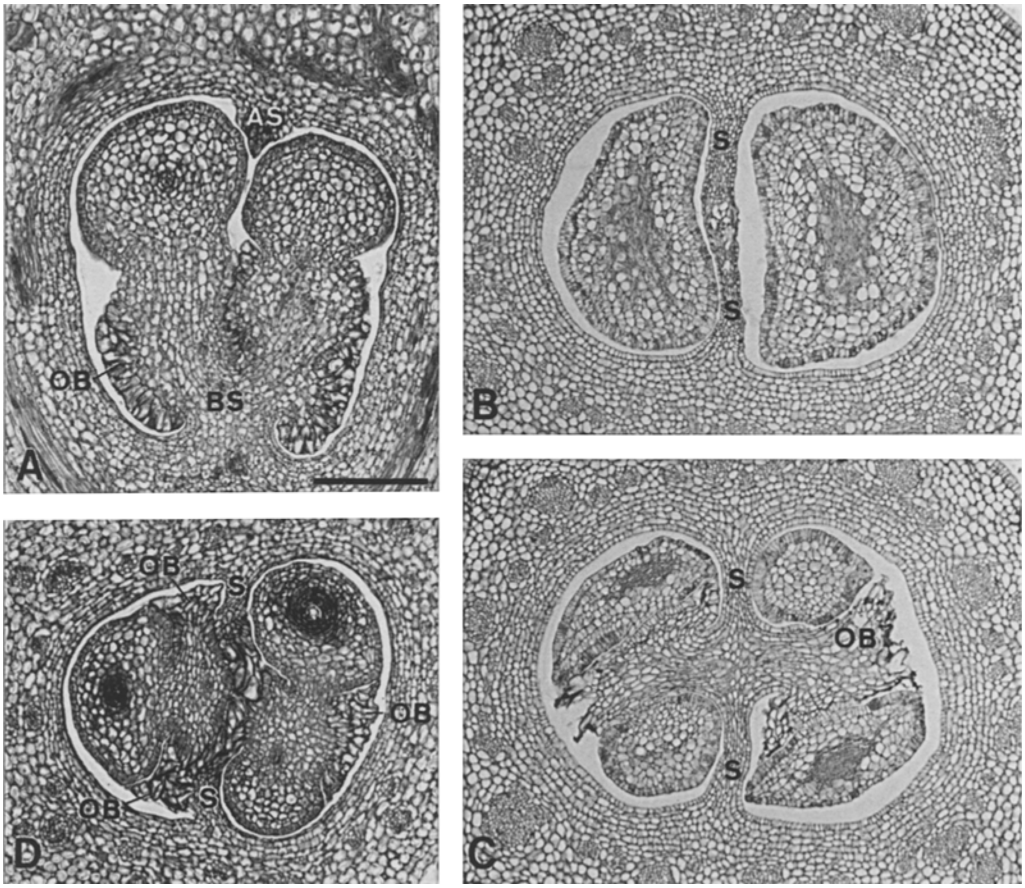


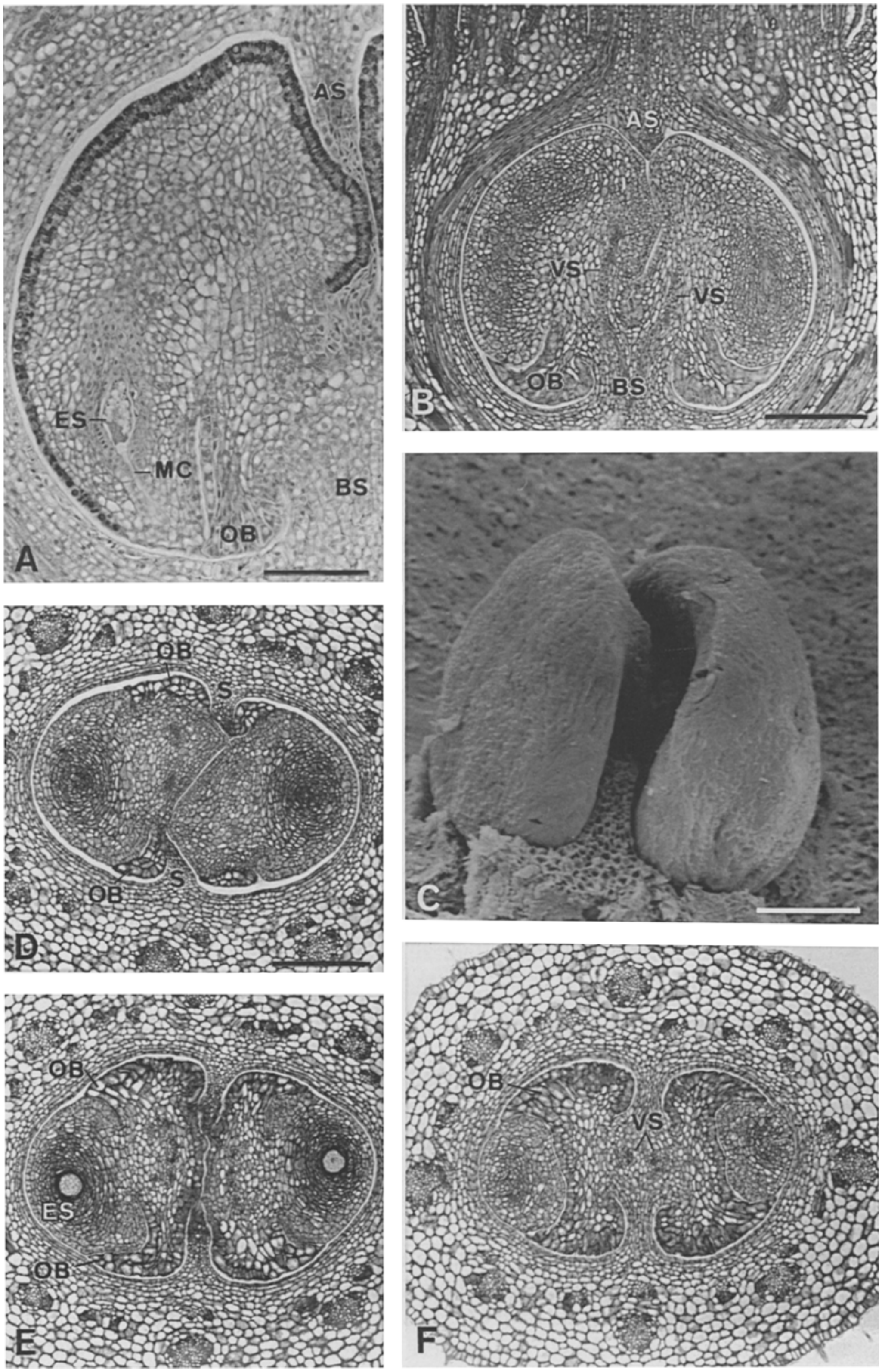
Fig. 1. *Rutidea*, ovule type I; ovary, placentation, and ovules. *A*, *Rutidea* spec., *B*, *C R. fuscescens* subsp. *bracteata*, *D R. insculpta*. *A* Longitudinal ovary section perpendicular to the septum; *B*, *C* ovary cross-sections at different levels, *B* high up and *C* near the base of the ovules (because of the ovule curvature each ovule is sectioned twice, levels of the sections corresponding to levels C, D indicated in Fig. 3 *B*); *D* cross-section through ovary with one ovule of ovule type I (right) and one of ovule type II (left). Bar for *A*–*D*: 0.2 mm. – *AS* Apical part of septum, *BS* basal part of septum, *OB* obturator, *S* septum

(ii) a rather thick, homogeneous zone of rounded to polygonal parenchymatic cells (the later mesocarp), and

(iii) three to four layers of elongated thin–walled cells lining the locules (the later endocarp).

In the species studied here, tannins were either absent in the ovary wall and the septum or restricted to the vicinity of the vascular bundles (which run in zone "ii"). Crystal sand was found in the parenchymatous layers of the future mesocarp (and also in the ovular tissue).

Invariably, the placentas of *Rutidea* are attached to the basal part of the septum, very near to the base of the ovary (Figs. 1 A, 2 B); descriptions like "ovules ascending from the base of the ovary", cf. Bridson (1978), are not fully accurate, as already mentioned by Robbrecht & Puff (1986). The large ovules, which are surrounded by an elaborate obturator (see below for further details), fill out most


AS
ES
MC
OB
BS
A
AS
VS
VS
OB
BS
B
C
OB
S
S
OB
D
OB
ES
OB
E
OB
VS
F

of the interior of the ovary, and as there is no continuous septum, they are often in direct contact with each other and tend to partly enter cross-wise into each others imaginary "locules" (Fig. 2 B–D).

Placentas and ovules are supplied by vascular bundles which run up from the base of the ovary. A solitary bundle first enters the basal part of the septum and then divides into two to supply both placentas (compare, for example, Fig. 2 F). The same vascularization pattern was also noted in the other *Pavetteae* investigated (Fig. 4 A, C).

Pollen transmitting tissue, coming down from the centre of the style, enters the ovary from the top and runs in the apical part of the septum. It is easily distinguished by its tissue structure and staining behaviour (being intensively stained blue with toluidinblue).

Anomalous trilocular ovaries with three ovules are only known from two *Rutidea* species, namely *R. membranacea* HIERN (already mentioned by HIERN 1877, reconfirmed in the present study) and *R. insculpta*. However, in both species they are so rare that a more detailed study was impossible. Nevertheless, it is very probable that they represent truly three-carpellate morphs (with a solitary ovule per carpel) rather than bicarpellate forms in which one carpel produces two instead of a single ovule. The presence of three instead of two stigma-lobes in such forms (cf. HIERN 1877, BRIDSON 1978) strongly supports this interpretation.

Ovule and obturator. The ovules of *Rutidea* are campylotropous (sensu BOUMAN & BOESEWINKEL 1991), a situation correctly (or at least partly so) described or depicted by some older authors (e.g., HIERN 1877: "amphitropous-subreniform"; DE WILDEMAN 1910: plate XCV) but not discussed by later authors, although the ovule structure is remarkable and rare within the tribe and even the family *Rubiaceae*.

In the following text three informal ovule types are distinguished. However, it must be noted that this distinction is made for convenience and that the ovules in *Rutidea* show an almost continuous range of variation. Furthermore, although the majority of ovules in one species is of one specific type, exceptions can be observed.

Typically, the ovule is strongly curved in several directions, resulting in a concave shape sessile on the basal placenta and obturator. The funicle is very short and situated at the basal side in the middle of the ovule. The chalazal and micropylar ends are bent downwards to the bottom of the ovary locule (Fig. 3 A), so that the raphal side is strongly concave. The obturator is situated at the basal side of the ovule, in between the concave part and as wings underneath the two ends of the

Fig. 2. *Rutidea*, ovule type II; ovary, placentation and ovules. *A, C Rutidea fuscescens* subsp. *bracteata, B, D–F R. fuscescens* subsp. *fuscescens. A* Longitudinal ovule section perpendicular to the septum (note embryo sac and micropylar canal); *B* longitudinal ovary section perpendicular to the septum (note apical and basal part of the septum); *C* SEM-graph, lateral view of ovule pair (note the ovules entering cross-wise in each others locule); *D–F* ovary cross-sections at different levels, *D* high up, *E* somewhat lower, *F* near base of ovules (levels of Fig. 2 *D, E* somewhat lower than level G indicated in Fig. 3 *F*; level of Fig. 2 *F* corresponding to level H indicated in Fig. 3 *F*). Bars: *A* 0.1 mm, *B* 0.2 mm; *C* 100 µm, *D, E, F* 0.2 mm. – *ES* Embryo sac, *MC* micropylar canal, *VS* vascular supply, other abbreviations as in Fig. 1

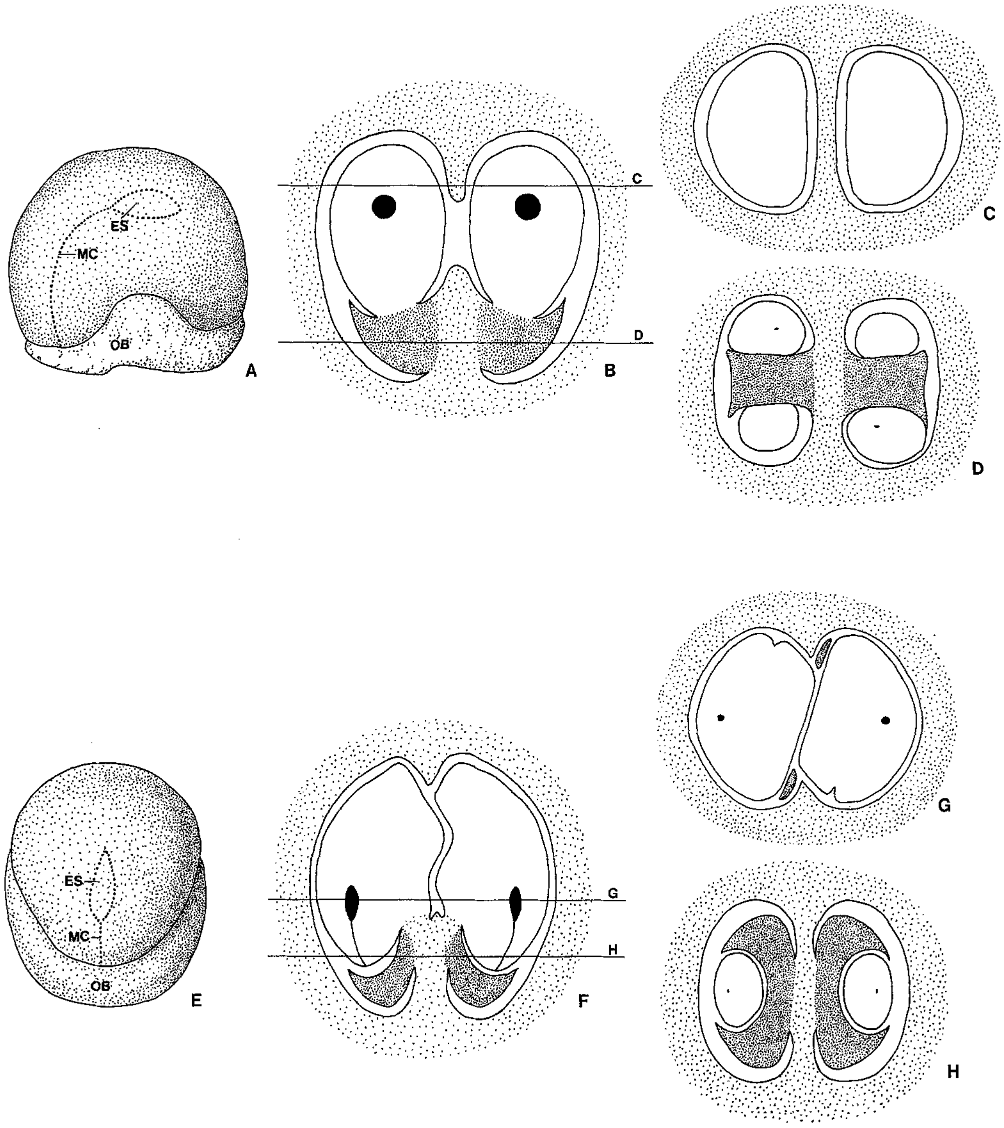


Fig. 3. *Rutidea*, semi-schematic ovary sections. *A–D* Ovule type I, *E–H* ovule type II. *A, D* Front views of ovules (abaxial side); *B, F* median longitudinal sections; *C, D, G, H* cross-sections at the levels indicated in *B* and *F*, respectively. – Shading of semi-schematic sections *B–D, F–H*: inner part of ovary wall, septum parts and placenta finely dotted, obturator heavily dotted, embryo sac and micropylar canal black. – Abbreviations as in Figs. 1, 2

ovule. As a result, the curved line that can be drawn through micropyle, embryo sac and chalaza is essentially in a horizontal position (or, in other words, at a right angle to the ovary's long axis). This situation will further on be referred to as "ovule type I" (Figs. 1 A–D, 3 A–D).

Within *Rutidea*, there is, however, some variation in the orientation of the ovule. In *R. fuscescens* subsp. *fuscescens*, for example, the line between micropyle and chalaza is in a vertical position (or, in other words, ± parallel to the ovary's long axis). This is referred to as "ovule type II". Often, the curving is not so strong as in ovule type I, and the abaxial and adaxial sides of the ovule are unequal in length, the latter being shorter. Here too the funicle is almost non–existent. The obturator is situated at the base and the sides of the ovule up to half of its height (Figs. 2 A–F, 3 E–H).

The two described ovule types, thus, differ in the orientation and degree of curving of the ovules, but it must be stressed that they are basically similar and that their distinction is not always clear–cut. The curving of the ovules appears to partly depend on the ovule orientation. Indeed, ovules of type II could be hindered by the presence of the small "apical" septum and by the other ovule in the second locule. The fact that sometimes (e.g., *R. fuscescens* subsp. *fuscescens, R. insculpta*) ovules of both type I and II are found within one ovary (Fig. 1 D), clearly shows that the two types morphologically can be derived from each other. Moreover, intermediate forms were observed in which the micropyle–chalaza line is neither horizontal nor vertical, but oblique.

In a few *Rutidea* species, such as *R. hispida*, the ovules are very small and less curved; their raphal side is hardly concave at all. This could be referred to as "ovule type III". Unfortunately, too little preserved material was at disposal for a full understanding of them. It is, however, very likely that they represent the original situation from which the typical ovule of *Rutidea* may be derived.

The ovules of *Nichallea* agree well with this type; although not curved when seen from the outside, they also exhibit the same trend to campylotropy as the type III ovules of *Rutidea* (Fig. 4 A).

The ovules are unitegmic. The epidermal layer of the integument (future exotesta) consists of columnar cells, which in some species contain tannin vesicles already in the ovule stage. The integument is very thick, so that there is a long and slender micropylar canal. Its lower part is somewhat curved towards the base of the septum and the micropyle itself is pointed downwards (Fig. 2 A). The opening of the micropylar canal is located in the immediate vicinity of the obturator tissue.

The embryo sac contains amylose grains (Fig. 2 A), as was also noted in other genera of the *Pavetteae* [e.g., *Dictyandra, Leptactina, Ixora, Pavetta* (Fig. 4 C)]; this phenomenon seems to be quite common in the *Rubiaceae* (also cf. FAGERLIND 1937).

The obturator tissue forms a ± annular and cushion–shaped structure embracing the base of the ovule. In longitudinal sections, it is observed as a massive wing or "finger" underneath the ovule and between the adaxial ovule base and the septum (Figs. 1 A, 2 A, B).

The development of the obturator starts at a very early developmental stage. Its tissue consists of large, thin-walled cells, polygonal to elongated in shape (Fig. 5 A). Obturator tissue is easily distinguished from the placental tissue, as it has a different consistency.

It is to be noted that *Nichallea* has an obturator structure and shape that is virtually identical to that of *Rutidea* (Fig. 4 A). Obturators of other genera of the *Pavetteae* have a different structure and shape: in *Ixora* and *Pavetta*, for example, there is a prominent, ± dish-shaped obturator developed both near the micropylar end and the chalazal side of the ovule (Fig. 4 B, C). In genera such as *Dictyandra, Leptactina* or *Tarenna*, the obturator is less massive and conspicuous, although

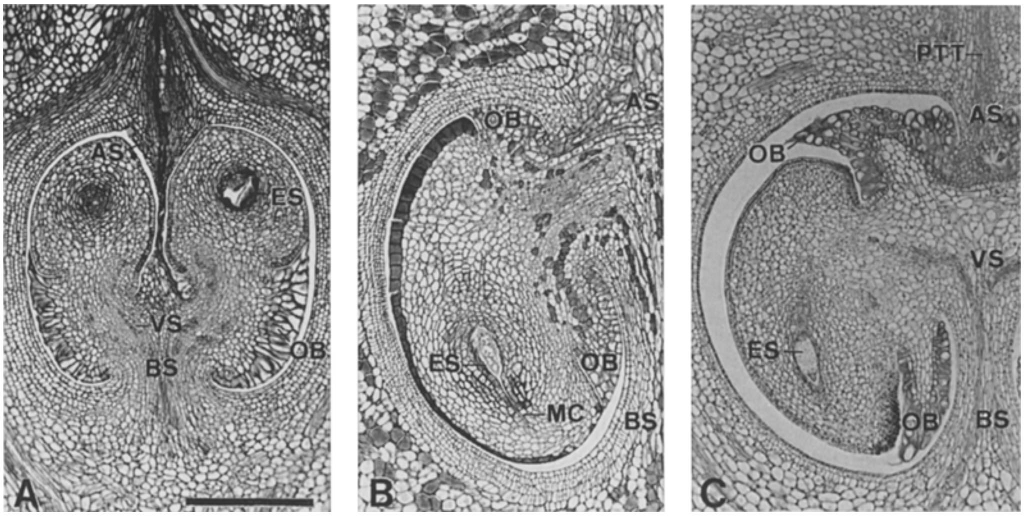
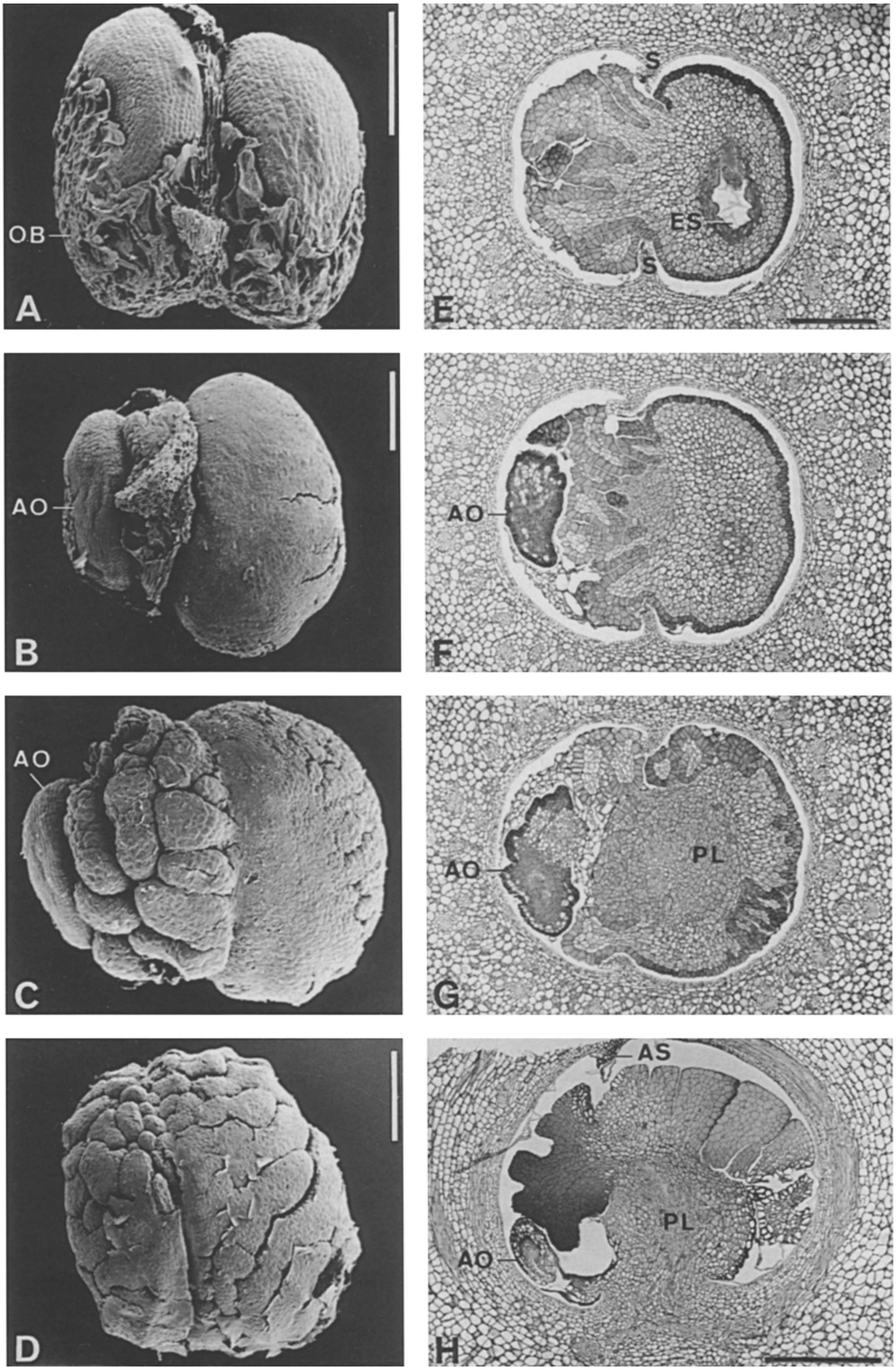


Fig. 4. *Pavetteae*, ovary, placentation and ovule of selected species. *A Nichallea soyauxii, B Ixora burundiensis, C Pavetta oliveriana. A* Longitudinal ovary section perpendicular to the septum (note the overall resemblance to the ovary of *Rutidea*); *B, C* longitudinal ovule sections perpendicular to the septum (note the well developed basal part of the septum, the small apical part and the obturator both below and above the ovule). Bar for *A–C* 0.3 mm. – *PTT* Pollen transmitting tissue, other abbreviations as in Figs. 1, 2

clearly recognizable as a cushion– or shallowly cup–shaped structure around the base of each ovule.

Seed development and rumination. The following description primarily refers to *Rutidea* species with "ovule type I" (see above), because preserved material of different developmental stages, necessary for a detailed anatomical account, was only available for species with this ovule type. The seed development pattern, studied in several species, proved to be largely similar in all of them. As noted before, only one of the two ovules of a *Rutidea* ovary will develop into a seed. The second ovule aborts in very early stages of fruit development (Fig. 5 B). It remains small and eventually shrivels; the developing seed pushes it to the side (Fig. 5 H) and envelops it, so that in mature fruits it may no longer be readily detectable.

Fig. 5. Seed development and ruminate seeds, *A–D, H Rutidea* spec., *E–G R. smithii* subsp. *submontana. A–D* Successive developmental stages; *A* paired ovules (anthesis), lateral view; *B* somewhat older stage (presumably after fertilization), aborted ovule (left) and developing seed (with first traces of rumination) as seen from above; C, older stage (developing seed from above), only raphal side with ruminations, aborted ovule largely hidden by them; *D* almost mature seed as seen from above, ruminations now present over the entire surface, the slightly off-centre groove corresponds to the septum area; *E–G* cross-sections through young fruit at different levels, *E* high up, *F* somewhat lower, *G* near the base of the seed, *H* median longitudinal section of young fruit (note the aborted ovule). Bars: *A–C* 200 µm, *D* 500 µm, *E–G* 0.3 mm, *H* 0.5 mm. – *AO* Aborted ovule, *PL* placenta, other abbreviations as in Figs. 1, 2


OB
A
S
ES
S
E
AO
B
AO
F
AO
C
AO
PL
G
D
AS
PL
AO
H

Soon after fertilization, the developing seed shows an overall increase in size (Fig. 5 B). This is the result of high meristematic activity in the inner layers of the integument; the cells show both anti- and periclinal divisions. In the epidermal layer of the integument (the future exotesta) two causes for expansion occur. Firstly, the cells enlarge excessively (Fig. 6 B); at the same time their tannin content increases. Secondly, anticlinal divisions take place, strongly concentrated at the raphal side of the ovule. This can be noticed under the binocular: the newly formed cells differ from the older ones in colour, as they are not yet totally filled with tannins. At the same time as the developing ovule/seed exhibits overall growth, the placenta enlarges and pushes upwards.

Probably due to the slow dilatation growth of the developing fruit, the rapidly dividing cells of the integumentary and chalazal tissues of the young seed lead to the production of folds and undulations within the limited space of the locule (Fig. 5 B, C). This occurs first at the raphal side of the developing seed where the tissues grow fastest (Fig. 5 C). The ruminations are initially strongest on the adaxial side of the developing seed which looks like having a cancerous outgrowth on this side (Fig. 5 C). As the septum is incomplete, the rapidly enlarging lobe–like ruminations soon start extending into the second locule (Fig. 5 E), covering and in time almost enveloping the aborted ovule (Fig. 5 C–H).

At that stage, the antiraphal (dorsal) side of the developing seed does not show cell division nor cell enlargement in the epidermal layer (Fig. 5 C). This part of the ovule/seed will only show ruminations at late stages of seed development. Note in this respect the difference in the size of the epidermal cells between ruminate and non–ruminate zones (Fig. 5 E).

The process of rumination thus takes place primarily in the thick integumentary tissue. The endosperm is not involved (except for the latest stages of development). As the ruminations originate in the thick integument, the endosperm stays quiescent as a small body in ± the centre of the developing seed. It does not grow out until the seed has almost reached its mature size. Only at that stage, the endosperm becomes meristematic, rapidly increasing in size and consuming all surrounding layers except those forming the seed-coat (Fig. 6 C).

From the above follows that the formation of the solitary, perfectly spherical seeds of *Rutidea* is a complicated process. While the ovules had already been strongly curved before fertilization, the developing seeds undergo further changes in shape: In order to be able to enter into and occupy the space of the second locule, they must curve in a direction perpendicular to the main curvature of the ovule (of ovule type I). The mature seeds fill up the space in both locules, which are no longer distinguishable as such–only the place of the original septum remains detectable (Figs. 5 H, 6 A, C).

The seeds have a narrow, somewhat obscured, but deep hilar cavity at their "base". This arises when, at an early stage in seed development, the basal part of the septum plus placenta grows upwards while the seed portions that laterally flank these tissues grow strongly downwards. These tissues (including the vascular strand in the interior) are therefore eventually ± fully and on all sides surrounded by the seed tissue.

The mature seeds are deeply ruminate over the whole surface. They show a network of folds and lobes in sections in every plane (Fig. 6 C, D). The term "laby-

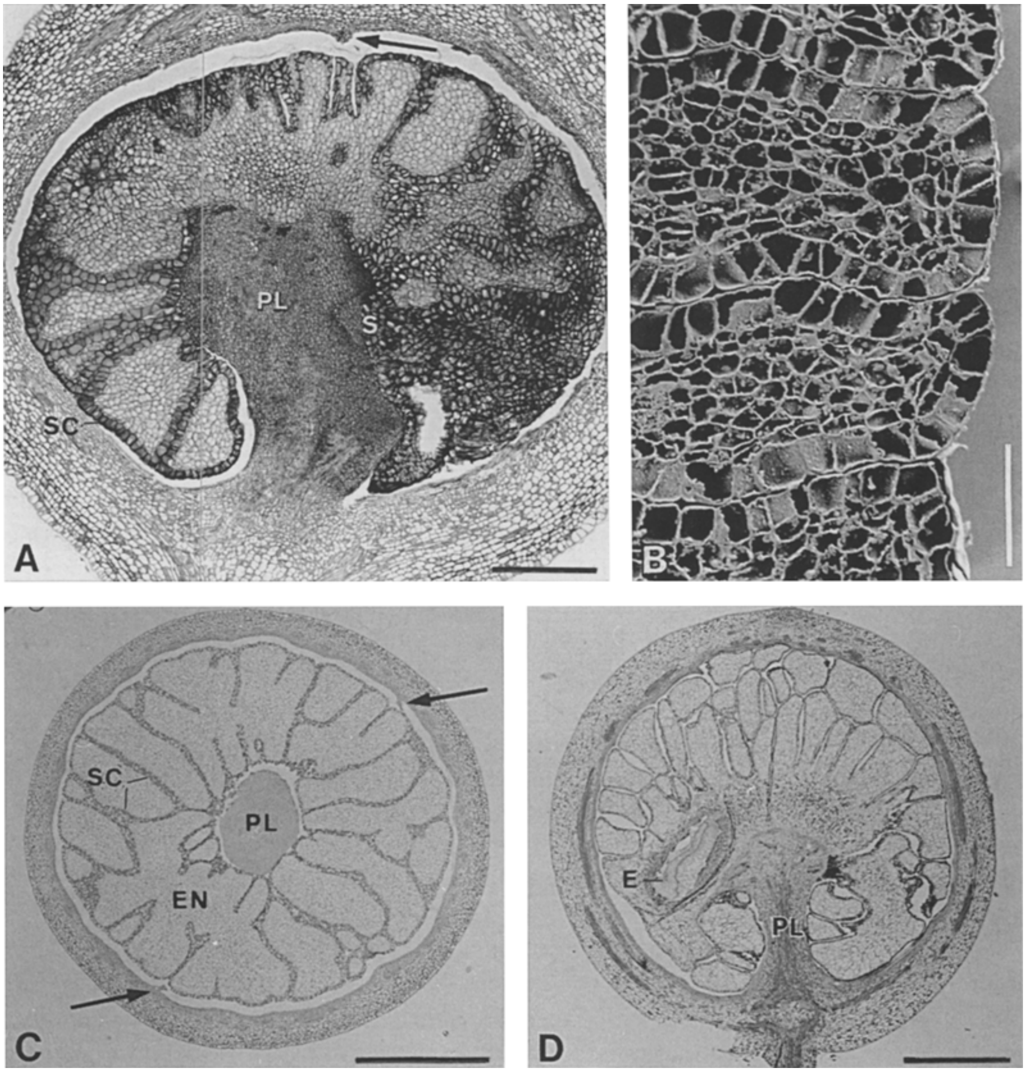


Fig. 6. Seed development and fruit, *A, C Rutidea smithii* subsp. *submontana*, *B, D Rutidea* spec. *A* Median longitudinal section of almost mature fruit, note minute apical septum (arrow); *B* SEM-graph, section through almost mature seed, note the large parenchymatic exotesta cells; *C* cross-section of lower half of mature fruit, note remnants of septum (arrows) plus placenta in the center; *D* median longitudinal section through mature fruit. Bars: *A* 0.5 mm, *B* 100 µm, *C, D* 2 mm. – *E* Embryo, *EN* endosperm, *SC* seed-coat, other abbreviations as in Figs. 1, 2

rinth seed", as introduced and defined by Van Heel (1970) is appropriate here (Van Heel 1970 defines labyrinth seeds as those seeds which, when cut in any plane, show a labyrinth structure; *Rutidea* would fall under his "Type i", i.e., deeply ruminate seeds with small cotyledons, which are not folded).

The embryo is found in a basically horizontal position in the not-ruminate central part of the seed, close to the placental tissue, and is somewhat curved (Fig. 6 D). Its maximum size is ± half of the width of the seed, but smaller embryos are common. The cotyledons are foliaceous, long and narrow (this form seems to be unusual in the tribe *Pavetteae*) and only slightly shorter than the cylindrical radicle (radicle : cotyledons ratio = 1 : 1.5). The orientation of the radicle varies from inferior to lateral.

The seed coat of the mature seed is exotestal. The exotesta is one-layered and consists of parenchymatic cells filled with tannins. The situation depicted for *Nichallea* (Bridson & Robbrecht 1985: fig. 2) is exactly the same. The cells of the several-layered endotesta are crushed by the growing endosperm and form an amorphous layer. Only in some of the folds or lobes, the endosperm does not encroach totally on the endotesta and leaves some cells intact. The endotestal cells are thin-walled and possess neither tannins nor crystals.

The endosperm is horny and has moderately thickened walls. In some species, e.g., *R. odorata* K. Krause and *R. fuscescens*, it contains small crystals (probably calcium oxalate).

Fruit. The fruits of *Rutidea* are drupes. They invariably are unilocular and always contain only a single, spherical seed as there is obligatory abortion of one of the ovules (see above for details).

In spite of the fruits being one-seeded, they are perfectly symmetrical in outer view (the same situation is, by the way, also encountered in the genus *Nichallea*). Abortion of ovules of one locule also does occur in other genera of the *Pavetteae*, but it is always an aberration and never a rule; such fruits are readily distinguished from “normal” fruits by their asymmetrical shape.

The exocarp is one-layered and consists of small parenchymatic cells covered with a rather thick cuticle. The mesocarp is comprised of several layers of large polygonal to rounded parenchymatic cells. It contains the massive vascular bundles (with a sheath of sclerenchymatic cells) which often cause the dried fruits to appear longitudinally ribbed.

The endocarp is made up of three to four layers of small fiber–like cells. Both their radial and tangential walls are extremely thickened, leaving only a small lumen that is usually filled with large hexaedrical crystals (probably calcium oxalate). The tissue is comparable to what Solereder (1893: 273) had described as “Kristallsklerenchym” (crystal sclerenchyma) in the bark, ovary wall or endocarp of various *Rubiaceae*, including the *Pavetteae* genera *Pavetta* and *Tarenna* (as *Webera*). In the course of the present study, crystal containing sclerenchyma was also noted in other *Pavetteae* genera, namely *Dictyandra* and *Leptactina*. Its absence in *Ixora*, already noted by Solereder (1893), could be confirmed.

In the fruit, the cells of the septum remnants are virtually inseparable in structure from those of the endocarp. The septum portions form a sclerenchymatic, inwardly projecting ridge on the inside of the endocarp (Fig. 6 C).

The stony endocarp has a preformed germination slit located basally on both sides of the hilar cavity and actually running along the thickened ridge formed by the peripheral portion of the septum. The endocarp is very vulnerable in this zone and ruptures easily when pressure is exerted. The embryo radicle in the seed points toward this zone. Thus one can easily imagine that, during germination, the elongating radicle will push open the endocarp in this region. The same opening mechanism is found in *Nichallea*, and preformed germination slits are also found in other genera of the tribe *Pavetteae*, e.g., in *Ixora*.

Discussion

Although unusual in some of the character states described above, *Rutidea* can nevertheless be easily accommodated in the *Pavetteae*:

Bicarpellate gynoecia as in *Rutidea* are typical for the tribe *Pavetteae*. Known exceptions are few: in the Mascarene genus *Myonima*, the ovary is 2- to 7-carpellate and in some *Ixora* species from Australia (ADAMS & al. 1987), Madagascar (GUÉDÈS 1986) and Tahiti (under the genus name *Hitoa*: BRIDSON & ROBBRECHT 1985), it is 3- to 4-carpellate. African taxa of the *Pavetteae*, however, are typically bicarpellate.

Carpels with a solitary ovule (uniovulate locules), as found in *Rutidea*, are also present in a number of other genera of the *Pavetteae* (*Ixora, Pavetta, Nichallea, Versteegia, Captaincookia, Myonima*, and *Duperrea*). However, in general, the tribe exhibits much variation in ovule number. The genera *Leptactina, Dictyandra*, and *Coleactina*, for example, are multiovulate, with the small ovules borne on large, U-shaped placentas. The remaining genera are pauciovulate, with the ovules either immersed in the placenta or pendulous.

With regard to placentation and ovule number, the paleotropical genus *Tarenna* s. l. is certainly the most variable taxon in the tribe: there are species with solitary ovules as well as taxa with pauci- to multiovulate placentas.

The great variation in ovule number resulted in the scattering of the genera of the tribe *Pavetteae* in different tribes (*Gardenieae* with more than one ovule per locule versus *Ixoreae* with one ovule per locule) in older classifications (e.g., HOOKER 1873, SCHUMANN 1891).

Septum structure also exhibits considerable variation in the genera of the *Pavetteae*. In general, this concerns extent and thickness of the basal part of the septum and of the apical septum. In *Ixora* and *Pavetta*, for example, the massive basal part of the septum extends very high up, and the apical septum is very short (Fig. 4 B, C); the placentas are inserted above the middle of the locules. In contrast, *Nichallea* has a very short and thick basal septum part and a very long apical septum (Fig. 4 A), and the placentas are attached near the base. This comes close to *Rutidea*, with the difference that in *Nichallea* the septum is continuous (direct contact between basal and apical septum).

Campylotropous ovules: The trend to this type of ovules seems to be common in the *Pavettae* but is otherwise rare in the family *Rubiaceae*. Campylotropous ovules had been reported for some distant genera, e.g., *Theligonum* (*The.*) (WUNDERLICH 1971), *Mitchella* and *Damnacanthus* (of uncertain tribal position) (ROBBRECHT & al. 1991) and *Schradera* (*Sch.*) (PUFF & al. 1993), but *Rubiaceae* ovules have mostly been described as anatropous.

The trend to hemianatropy and campylotropy is nevertheless probably more general than at present accepted. IGERSHEIM (1993 b) described the ovules of the *Vanguerieae* as anatropous, but at least some representatives of the tribe have ovules matching BOUMAN's (1984) definition of hemianatropy (nucellus forming an angle of 90° with the funicle), e.g., *Rytigynia kigeziensis* VERDC. (IGERSHEIM 1989: fig. 21 A, reproduced in ROBBRECHT 1988: fig. 38 B) or *Vangueria infausta* BURCHELL (IGERSHEIM 1993 b: fig. 5 I). Further, IGERSHEIM & ROBBRECHT (1993: fig. 2 D) describe the ovules of *Prismatomeris beccariana* (BAILL.) J. T. JOHANSSON as basically hemianatropous, but with a slight tendency to campylotropy, in that the embryo sac and the micropylar canal are rather strongly curved.

Apart from *Rutidea* and *Nichallea*, at least another two genera of the tribe *Pavetteae* possess campylotropous ovules borne in large numbers on a U-shaped placenta, namely *Dictyandra* and *Leptactina*. The situation is much the same as described and depicted for *Schradera* by Puff & al. (1993: figs. 6, 7). Further study of less known genera in the tribe *Pavetteae* might well reveal other genera with campylotropous ovules.

Consequently it seems that in the *Rubiaceae* hemianatropous and campylotropous ovules occur more often than hitherto accepted and with a range of intermediate states.

Rumination. Ruminate seeds are rare in the *Rubiaceae* and are, so far, only known from 14 genera (out of a total of 637 in the family). Two genera, namely *Schizenterospermum* (*Pav.*) and *Pubistylus* (*Oct.*), are to be added to the 12 genera listed by Robbrecht (1988).

In the *Pavetteae*, four (of a total of 20) genera have ruminate seeds: *Rutidea, Nichallea, Schizenterospermum*, and *Tarenna* (partly).

With regard to the morphological expression of the rumination, there is a considerable variation among the rubiaceous genera. Rumination is most pronounced in *Rutidea*, and the genus was even named for it (the generic name is derived from the Greek words "ρυτις" and "ιδος", which means wrinkle or fold; De Candolle 1807).

Nichallea is similar to *Rutidea*: the always unilocular fruit has a solitary, perfectly spherical seed which fills out the space of the former two locular cavities (as in *Rutidea*, the second ovule aborts in an early stage). In *Nichallea*, however, the seed is only partially ruminate, showing folds and undulations only at the basal part, around the hilar cavity. Although the seed development in *Nichallea* could not be studied due to lack of preserved material, the overall similarity of ovary and fruit structure between *Nichallea* and *Rutidea* supports the assumption that the process may be congruent in both genera.

In *Tarenna*, only about 10% of the species show rumination, and the fruits and seeds exhibit a wide range of morphological variation. Ruminate seeds occur in Asiatic species with two-locular fruits and always more than one seed (and sometimes very many seeds) per locule. The seeds are small and angular and their shape depends on the seed number; their rumination is usually very shallow. In all African *Tarenna* species with ruminate seeds, however, the fruits contain only one large spherical seed, which is deeply to shallowly or partially ruminate. At first sight, the impression arises that this situation closely resembles that in *Rutidea* and *Nichallea*, but the African ruminate *Tarenna* species differ markedly in detailed structure: the fruits are not unilocular but possess a continuous septum which, however, is pushed against the wall of the endocarp by the developing seed in one of the two locules; the second locule (with an aborted ovule) thus becomes totally squashed and flattened.

In *Schizenterospermum*, the fruits are reported to contain one large, deeply ruminate seed (Arènes 1960). Further information is unfortunately not available.

Studies on the process of rumination in the *Rubiaceae* are rare and have so far only been carried out on *Psychotria* spp., *Benkara malabarica* Lamk. (as *Randia* *malabarica* Periasamy 1965) and *Tarenna asiatica* (Linn.) Sant. & Merch. (Periasamy & Parameswaran 1965).

Periasamy (1962) thoroughly investigated the phenomenon of rumination in more than thirty families of seed plants and presented a classification of the rumination process. He distinguished seven types, based on the cause of rumination development but also on the structure of the ovule, the mature seed and the seedcoat. According to his classification, rumination in *Rubiaceae* belongs to the *Spigelia* type, which is also found in the *Loganiaceae, Caprifoliaceae, Apocynaceae*, and *Araliaceae*. The *Spigelia* rumination type is characterized by: (i) A unitegmic ovule. (ii) A one-layered seed coat. (iii) Folds and undulations in the seed coat (visible from the outside). (iv) Late endosperm development. (v) Chalazal hypertrophy: The chalaza shows an overall increase in size and occupies a relative greater part of the seed after fertilization. In the present study, the boundary between chalazal and integumentary tissue was never clearcut (the ovules of the *Rubiaceae* being unitegmic and tenuinucellate). Therefore, this criterion of Periasamy could not be applied to the present group. (vi) Ruminations preformed by the seed coat. The irregularities in the seed coat occur before the endosperm starts its expansion and cause the chalazal and integumentary tissues to be ruminate. Later the endosperm shows excessive meristematic and even unequal peripheral activity and becomes ruminate by growing into the infoldings and undulations of the seed coat, occupying all the available space.

The kind of rumination found in *Rutidea* agrees well with this type.

General conclusion

Although *Rutidea* differs from the other genera of the *Pavetteae* in the unusual features described above and also in its lianescent habit and the sometimes divided interpetiolar stipules, it nevertheless does not seem justified to remove the genus from the tribe. As shown above, many of the unusual character states can be derived from those of other *Pavetteae* and, therefore, represent an extension or fall into the range of variation found in the tribe.

The obtained data, moreover, provide further support for the previously suggested close relationship between *Rutidea* and the shrubby monospecific African genus *Nichallea* (Bridson & Robbrecht 1985).

Mostly on account of the similarity in fruit and ruminate seed, Bridson & Robbrecht (1985) had placed the genus pair *Rutidea* and *Nichallea* near *Tarenna*. African species of the latter have, however, a rather different placentation, and–as far as it can be judged at present–the mode of fruit and seed development appears to be different. More detailed anatomical studies of the ovary, fruit and seed of *Tarenna* and other genera of the *Pavetteae* are necessary for a better understanding of the relationships within the tribe.

Samples of preserved material were kindly provided by the herbarium curator of WAG and by Prof. C. Puff (University of Vienna). I am grateful to Prof. Puff and to my promotor Prof. E. Robbrecht for their supervision and their help in preparing this manuscript. Dr A. Igersheim (University of Vienna) kindly made most S.E.-micrographs (Figs. 5 A–D, 6 B). Various other people have contributed in various ways to this paper: Prof. E. Smets and D. Clinckemaillie (University of Leuven), Dr U. Rohrhofer (University of Vienna) and M. Verhaegen (National Botanic Garden of Belgium). – The study was carried out while holding a grant as Research Assistant of the National Fund for Scientific Research (Belgium); my stay in Vienna was possible because of a grant of the Austrian „Bundesministerium für Wissenschaft und Forschung", for which I hereby express my gratitude.

References

Adams, L. G., Bridson, D. M., Robbrecht, E., 1987: The identity of *Lasianthus graciliflorus* Bailey (*Rubiaceae*). – Kew Bull. **42**: 209–214.

Arènes, J., 1960: A propos de quelques genres malgaches de Rubiacées (Vanguériées et Gardeniées). – Notulae System. **16**: 6–19.

Bouman, F., 1984: The ovule. – In Johri, B. M., (Ed.): Embryology of angiosperms, pp. 123–157. – Berlin, Heidelberg, New York, Tokyo: Springer Verlag.

– Boesewinkel, F. D., 1991: The campylotropous ovules and seeds, their structures and functions. – Bot. Jahrb. Syst. **113**: 255–270.

Bridson, D., 1978: A short revision of *Rutidea* (*Rubiaceae*). – Kew Bull. **33**: 243–278.

– Robbrecht, E., 1985: Further notes on the tribe *Pavetteae* (*Rubiaceae*). – Bull. Natl. Plantentuin Belg. **55**: 83–115.

De Candolle, A. P., 1807: Mémoire sur le *Cuviera*: genre nouveau de la famille des Rubiacées. – Ann. Mus. Hist. Nat. **9**: 216–222.

De Wildeman, E., 1910: *Rutidea lujae* De Wild. nov. sp. – Pl. Nov. Herb. Hort. Then. **2**: 112–114, pl. 95.

Fagerlind, F., 1937: Embryologische, zytologische und bestäubungsexperimentelle Studien in der Familie *Rubiaceae* nebst Bemerkungen über einige Polyploiditätsprobleme. – Acta Horti Bergiani **11**: 195-470.

Guédès, M., 1986: Ixoras Malgaches nouveaux à fleurs solitaires. – Phytologia **60**: 243–250.

Hiern, W. P., 1877: Order LXX. *Rubiaceae*. – In Oliver, D., (Ed.): Flora of tropical Africa **3**, pp. 33–247. – London: Reeve.

Hooker, J. D., 1873: Ordo LXXXIV. *Rubiaceae*. – In Bentham, G., Hooker, J. D., (Eds): Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata defirmata **2**, pp. 7–151. – London: Reeve.

Igersheim, A., 1989: Beiträge zur Klärung der Gattungsabgrenzungsprobleme innerhalb der *Rubiaceae-Vanguerieae*. – Ph.D. Thesis, University of Vienna, Austria.

– 1993 a: The character states of the Caribbean monotypic endemic *Strumpfia* Jacq. (*Rubiaceae*). – Nordic J. Bot. **13**: 545–559.

– 1993 b: Gynoecium development in *Rubiaceae-Vanguerieae*, with particular reference to the "stylar-head"–complex and secondary pollen presentation. – Pl. Syst. Evol. **187**: 175–190.

– Robbrecht, E., 1993: The character states and relationships of the *Prismatomerideae* (*Rubiaceae-Rubioideae*). Comparisons with *Morinda* and comments on the circumscription of the *Morindeae* s. str. – Opera Bot. Belg. **6**: 61–79.

Periasamy, K., 1962: The ruminate endosperm: development and types of rumination. – In: Plant embryology. A symposium, pp. 62–74. – New Delhi: Council of Scientific & Industrial Research.

– 1965: Studies on seeds with ruminate endosperm.V. Seed development and rumination in two genera of the *Rubiaceae*. – Proc. Indian Acad. Sci., Sect. B, **60**: 351–360.

– Parameswaran, N., 1965: A contribution to the floral morphology and embryology of *Tarenna asiatica*. – Beitr. Biol. Pflanzen **41**: 123–138.

Puff, C., Andersson, L., Rohrhofer, U., Igersheim, A., 1993: The tribe *Schradereae* (*Rubiaceae*) reexamined. – Bot. Jahrb. Syst. **114**: 449–479.

Robbrecht, E., 1988: Tropical woody *Rubiaceae*. – Opera Bot. Belg. **1**: 1–271.

– 1993: Advances in *Rubiaceae* macrosystematics. Introduction. – Opera Bot. Belg. **6**: 7–18.

– Puff, C., 1986: A survey of the *Gardenieae* and related tribes (*Rubiaceae*). – Bot. Jahrb. Syst.: **108**: 63–117.

– – Igersheim, A., 1991: The genera *Mitchella* and *Damnacanthus*. Evidence for their close alliance; comments on the campylotropy in the *Rubiaceae* and the circumscription of the *Morindeae*. – Blumea **35**: 307–345.

Schumann, K., 1891: *Rubiaceae*. – In Engler, A., Prantl, K., (Eds): Die natürlichen Pflanzenfamilien **4 (4)**: 1–156. – Leipzig: Engelmann.

Solereder, H., 1893: Ein Beitrag zur anatomischen Charakteristik und zur Systematik der *Rubiaceen*. Fortsetzung. – Bull. Herb. Boissier **1**: 269–286.

Van Heel, W. A., 1970: Some unusual tropical labyrinth seeds. – Proc. Koninkl. Nederland. Akad. Wet. C **73**: 298–301.

Wunderlich, R., 1971: Die systematische Stellung von *Theligonum*. – Österr. Bot. Z. **119**: 329–394.

Address of the author: Petra De Block, National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium.

Accepted September 16, 1994 by A. Weber