



*Botanical Journal of the Linnean Society*, 2013, **172**, 404–448. With 29 figures

# Comparative floral structure and systematics of the clade of Lophopyxidaceae and Putranjivaceae (Malpighiales)

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*Received 30 October 2012; revised 31 January 2013; accepted for publication 3 March 2013*

In molecular phylogenetic studies, Lophopyxidaceae and Putranjivaceae are well supported as sisters in the large rosid order Malpighiales. As the floral structure of both families is poorly known and the two families have never been compared, the present comparative study was carried out, as part of a larger project on the comparative floral structure of Malpighiales, using microtome section series and scanning electron microscopy (SEM) studies. Similar to other angiosperm clades, it appears that the structure of the ovules is a strong marker for suprafamilial relationships in Malpighiales. Both families have two **collateral pendant antitropous ovules per carpel associated with obturators** (as in some Euphorbiaceae *s.l.*, to which Putranjivaceae belonged in earlier classifications). However, in contrast with Euphorbiaceae *s.l.*, the ovules are not crassinucellar, but either incompletely tenuinucellar or only weakly crassinucellar with a long and conspicuously slender nucellus and an endothelium, and do not have a nucellar beak, but a normal micropyle, features they share with families other than Euphorbiaceae *s.l.* among Malpighiales. Other shared features of the two families include the following. The outer sepals tend to be smaller than the inner ones and the sepals do not protect the gynoecium in older buds. Sepals of some taxa have a single vascular trace. A short zone of synsepaly tends to be present. Stamens tend to be antesepalous in haplostemonous flowers. A short gynophore is present. The synascidiate zone extends up to above the placenta, but is restricted to the ovary in taxa with more than one carpel. The micropyle is formed by the inner integument. The ventral carpel slits extend down into the synascidiate zone as postgenitally fused furrows. The carpels have a broad dorsal band of vascular bundles in the style. The overall floral structure of the two families corroborates their sister position well and does not support the earlier association of Putranjivaceae with Euphorbiaceae *s.l.* or of Lophopyxidaceae with Geraniales–Sapindales–Celastrales, which rely on shared superficial floral similarities.

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**ADDITIONAL KEYWORDS:** androecium – core eudicots – Euphorbiaceae – floral anatomy – floral morphology – Geraniales – gynoecium – perianth – Phyllanthaceae – Picrodendraceae – rosids.

## INTRODUCTION

Molecular systematic studies over the past two decades have revealed completely new topologies for the phylogenetic relationships of flowering plants. These findings have resulted in a profound rearrangement of taxonomic groups at all levels of the systematic hierarchy. Of special interest are the suprafamilial levels. New orders and new families have appeared and old orders have changed in the

content of their families, as reviewed, for example, in Chase, Fay and Savolainen (2000), Savolainen *et al.* (2000), APG III (2009) and Endress & Matthews (2012).

It has also become apparent that such new orders are unknown in both their morphology and biology, as, to date, their systematic components have never been studied comparatively. Similarly, the new families are also often unknown in these details as their genera were often hidden in larger earlier families, and thus went almost unnoticed, and are only now being exposed following molecular phylogenetic

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studies. Thus, it is urgent that comparative studies of these new families and newly circumscribed orders and supraordinal clades are carried out (Endress & Matthews, 2006, 2012; Endress, 2010). For this purpose, we began a series of comparative investigations in the large group, rosids, at the level of orders, such as Oxalidales (seven families; Matthews *et al.*, 2001; Matthews & Endress, 2002), Cucurbitales (seven families; Matthews *et al.*, 2001; Matthews & Endress, 2004), Celastrales (three families; Matthews & Endress, 2005a) and Crossosomatales (seven families; Matthews & Endress, 2005b). We also began to tackle the largest order of rosids, the giant Malpighiales, with c. 40 families (Wurdack & Davis, 2009; Xi *et al.*, 2012). Here, we focused on suprafamilial clades that were well resolved and well supported in the phylogeny that was current at the time. For Malpighiales, we began with Chrysobalanaceae and relatives (five families; Merino Sutter & Endress, 2003; Matthews & Endress, 2008), followed by Rhizophoraceae and potentially related families (seven families; Matthews & Endress, 2011), and Ochnaceae s.l. (three previously recognized families; Matthews, Amaral & Endress, 2012). In addition, we presented a survey of the current knowledge of floral structure across Malpighiales (Endress, Davis & Matthews, 2013). The present work on the poorly known families Lophopyxidaceae and Putranjivaceae and the recently recognized clade they form is a further contribution to this series of studies.

Lophopyxidaceae consists of the sole genus *Lophopyxis* Hook.f. with one or two species (Sleumer, 1971). The floral structure is poorly known, probably because the flowers are hairy and rich in tannins, making them technically difficult for microtome sectioning. Putranjivaceae has one to three genera: *Drypetes* Vahl (with c. 200 species in the Old and New World Tropics; Pax & Hoffmann, 1921; Webster, 1994b), *Putranjiva* Wall. (with four or five species in Asia; Webster, 1994b) and *Sibangea* Oliv. (with three species in tropical Africa, Radcliffe-Smith, 1976; Webster, 1994b). Members of Putranjivaceae are also not well known in their floral structure, but there have been several embryological studies on *Putranjiva* and *Drypetes* (Banerji & Dutt, 1944; Thathachar, 1953; Singh, 1970; Tokuoka & Tobe, 1995, 1999).

A systematic affinity between Lophopyxidaceae and Putranjivaceae was never assumed in the premolecular era. Only in the *rbcL* analysis by Wurdack *et al.* (2004) was a sister relationship of Lophopyxidaceae and Putranjivaceae first found (but with only nine families of Malpighiales included in the analysis and with weak support). This was followed by a four-locus/124-taxon study by Davis *et al.* (2005) (with all families of Malpighiales included in the analysis), and later confirmed with good support by a 13-locus/144-

taxon study (Wurdack & Davis, 2009) and with strong support by a 17-locus/640-taxon (angiosperm-wide) study (Soltis *et al.*, 2011) and an 82-locus/58-taxon study (Xi *et al.*, 2012).

## MATERIAL AND METHODS

### TAXA EXAMINED AND MICROSCOPY

Open flowers and floral buds of both families (Table 1), fixed in formalin–acetic acid–alcohol (FAA) or 70% ethanol (see Table 1 for dry material), were used for light microscopy (LM) and scanning electron microscopy (SEM). Dry herbarium material was rehydrated and softened using sodium bis(2-ethylhexyl) sulfosuccinate (Fluka) at c. 20 °C (Erbar, 1995). For the serial microtome sections (transverse and longitudinal sections), specimens were embedded in Kulzers Technovit 7100 (2-hydroethyl methacrylate). A stepwise infiltration was conducted to enhance infiltration with the following ratios of 100% ethanol to Technovit solution (50 : 50, 25 : 75, 0 : 100). Embedded material was sectioned using a Microm HM 355 rotary microtome with a conventional knife D. The 6-µm-thick sections were stained with ruthenium red and toluidine blue, and mounted in Histomount. For SEM studies, specimens were post-fixed in 2% osmium tetroxide (Fluka), dehydrated in ethanol and acetone, critical point dried, sputter coated with gold and examined with a Joel 6360LV scanning electron microscope. Permanent slides of the microtome sections and SEM material were deposited at the Institute of Systematic Botany, University of Zurich, Switzerland (Z).

### FLORAL DESCRIPTIONS AND LINE DRAWINGS

The floral structure is described for one species of the mono- or ditypic family Lophopyxidaceae and for selected representatives from all three genera of Putranjivaceae, including representatives of *Drypetes* from different geographical regions. For each species, at least one floral bud and two anthetic gynoecia (one sectioned transversely and the other longitudinally) were sectioned. In addition, a number of flowers were dissected and studied under both dissecting and scanning electron microscopes. Only in male *Drypetes gossweileri* S.Moore was a single bud studied because of limited material; this is indicated in Table 1. The gynoecium for all taxa is described at anthesis (unless otherwise indicated). The description of all other floral parts (unless otherwise mentioned) is based on advanced floral buds (in which male meiosis has taken place). This stage was preferred over anthetic flowers as the perianth organs are still in an upright position and thus entire flowers could be studied in transverse section series. Flowers are generally

**Table 1.** List of taxa and specimens studied (herbaria acronyms are given in square brackets)

Taxa studied	Sex	Floral stage	Material	Collection details
<b>Lophopyxidaceae</b>				
<i>Lophopyxis maingayi</i> Hook.f.	Male and female	Buds; open flowers	Liquid-fixed	<i>H.J. Lam</i> 3014 (Sulawesi, Indonesia); [L]
<b>Putranjivaceae</b>				
<i>Drypetes amazonica</i> Steyermark.	Male	Buds; open flowers	Dry	<i>J.R.I. Wood</i> 14958 (Bolivia); [K]
<i>Drypetes deplanchei</i> (Brongn. & Gris) Merr.	Female	Buds; open flowers	Liquid-fixed	<i>B. Gray</i> 5357 (Queensland, Australia); [CNS] (Fig. 78); <i>P.I. Forster</i> PIF7679 (Queensland, Australia); [BRI] (Figs 4, 5, 68, 79, 95, 103, 104)
	Male	Buds; open flowers	Liquid-fixed	<i>B. Gray</i> 2304 (Queensland, Australia); [CNS]
<i>Drypetes gossweileri</i> S. Moore	Female	Open flowers; post-anthetic flowers	Liquid-fixed	<i>J.P.M. Brenan</i> 8474 (Nigeria); [K]
	Male	Buds; open flowers	Liquid-fixed	<i>D.J. Harris &amp; J.M. Fay</i> JM 39 (Central African Republic); [K]
<i>Drypetes lateriflora</i> Krug & Urb.	Female	Buds; open flowers	Dry	<i>C.L. Lundell</i> 16581 (Guatemala); [K]
<i>Drypetes longifolia</i> Pax & K.Hoffm.	Male	Buds	Liquid-fixed	<i>M.J.E. Coode</i> 5345 (Philippines); [L]
<i>Drypetes madagascariensis</i> (Lam.) Humbert & Leandri	Female	Buds; open flowers	Dry	<i>G. McPherson</i> 14605 (Fort Dauphin, Madagascar); [MO]
	Male	Buds; open flowers	Dry	<i>G. McPherson</i> 14576 (Fort Dauphin, Madagascar); [MO]
<i>Drypetes vernicosa</i> P.I.Forst.	Female	Open flowers	Liquid-fixed	<i>B. Gray</i> 6876 (Queensland, Australia); [CNS]
	Male	Buds; open flowers	Liquid-fixed	<i>B. Gray</i> 6877 (Queensland, Australia); [CNS]
<i>Drypetes</i> sp.	Male and female	Buds (male); post-anthetic (female)	Liquid-fixed	<i>H.P. Nooteboom</i> 5882 (Indonesia); [L]
<i>Putranjiva roxburghii</i> Wall.	Female	Buds; open flowers; post anthetic flowers	Liquid-fixed	<i>K. Seshagirirao &amp; V.S. Raju</i> 1022 (Hyderabad, India); [UH]
	Male	Very young buds; advanced buds; open flowers	Liquid-fixed	<i>K. Seshagirirao &amp; L. Harikrishnanai</i> 1025 (Hyderabad, India); [UH]
<i>Sibangea arborescens</i> Oliv.	Female	Buds; open flowers	Liquid-fixed	<i>F.J. Breteler</i> 13205 (Gabon); [WAG] (Figs 17, 40, 70, 81, 82, 87, 88, 101, 102); <i>F.J. Breteler</i> 15525 (Gabon); [WAG] (Fig. 16)
	Male	Buds; open flowers	Dry	<i>J.J.F.E. de Wilde</i> 7962 (Cameroon); [WAG]

described from the apex downwards. The course of the pollen tube transmitting tract (PTTT) is described in the morphology section for practical reasons. The integument thickness is measured in anthetic ovules at the level of the mid-length of the nucellus.

Line drawings of transverse sections of buds and anthetic gynoecia represent actual sections within a bud or anthetic gynoecium. They were prepared on the basis of photographed section series, which incorporated structurally relevant levels in the

flower. Based on these sections and in conjunction with careful checking of the actual section on the microscope (especially for details of the vasculature, postgenital fusion within the gynoecium and the pathway of the PTTT), each section was carefully traced at high magnification in Adobe Illustrator using a Wacom tablet and pen. All morphological surfaces (thicker lines) and vasculature (thinner lines) were included in the drawn sections; postgenital fusion was represented by broken lines, and the PTTT and nectary tissue were represented by light and dark grey shading of the tissue. In contrast with the transverse section series, the median longitudinal sections represent a schematic section through the median longitudinal plane of the gynoecium, and comparatively display the plicate, symplicate and synascidiate zones, including details of the pathway of the PTTT, location of the compitum and zones of postgenital fusion. These diagrams were based on a composite of actual longitudinal sections of the gynoecia, which were modified to represent the 'ideal' section and have been further adjusted to correspond to the actual transverse sections at the relevant level in the gynoecium.

#### GLOSSARY

*Angiospermy types (mode of carpel or gynoecium closure).* Type 1: angiospermy by secretion. Type 2: angiospermy by a continuous (secretory) canal and partial postgenital fusion of the periphery. Type 3: angiospermy by a partial canal and postgenital fusion along the entire length of the ventral slit at the carpel periphery. Type 4: angiospermy by postgenital fusion along the entire length of the ventral slit (see also Endress & Iggersheim, 2000).

*Antitropous ovule curvature direction.* Antitropous ovules are curved in the reverse direction to carpels (see also Endress, 2011a).

*Euphorbiaceae s.l..* This is used here in the sense of the earlier, classical circumscription (including Euphorbiaceae, Phyllanthaceae, Picodendraceae, Peraceae, Putranjivaceae, e.g. Cronquist, 1981), and not to describe the clade as it is currently circumscribed (e.g. Xi *et al.*, 2012).

*Flower size (open flowers).* Length from the lower part of the floral base to the tip of the stigma. Flowers generally range from small ( $\leq 5$  mm) to medium sized (up to c. 15 mm) (see also Matthews & Endress, 2011).

*Gynophore.* Short or longer basal extension of the gynoecium below the locules.

*Ovules weakly crassinucellar and incompletely tenuinucellar.* In weakly crassinucellar ovules, there is only a single hypodermal cell layer above the meiocyte at the nucellus apex. In incompletely tenuinucellar ovules, there is no hypodermal cell layer above the

meiocyte at the nucellus apex, but there is hypodermal tissue at the flanks and/or below the meiocyte (see also Endress, 2011a).

*Shape of floral base.* This expresses the shape of a virtual plane through the attachment areas of all floral organs, which can be flat, convex or concave.

*Special mucilage cells.* Cells with the inner or outer periclinal wall thickened by layered mucilage (see also Matthews & Endress, 2006).

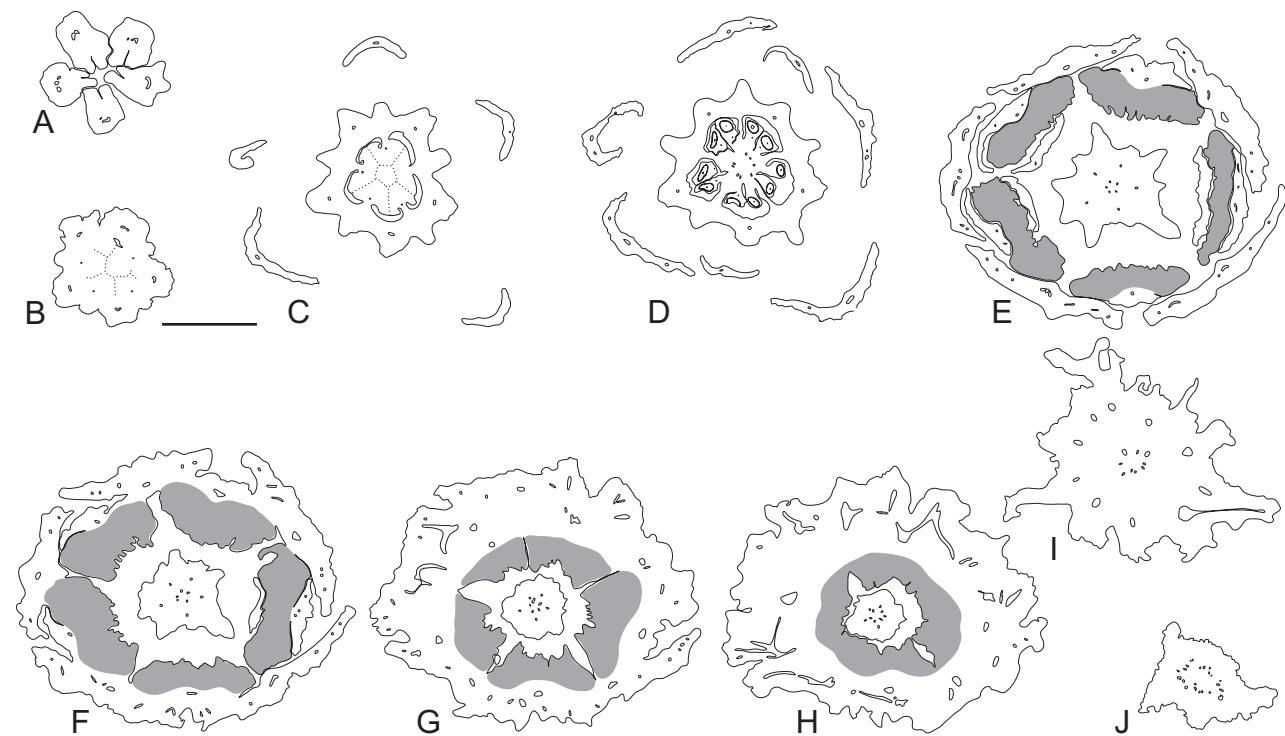
## RESULTS

### LOPHOPYXIDACEAE

*Lophopyxis maingayi (female)*

Figures 1, 2, 19, 20, 31, 32, 38, 63, 71, 72, 83, 84, 96, 109A.

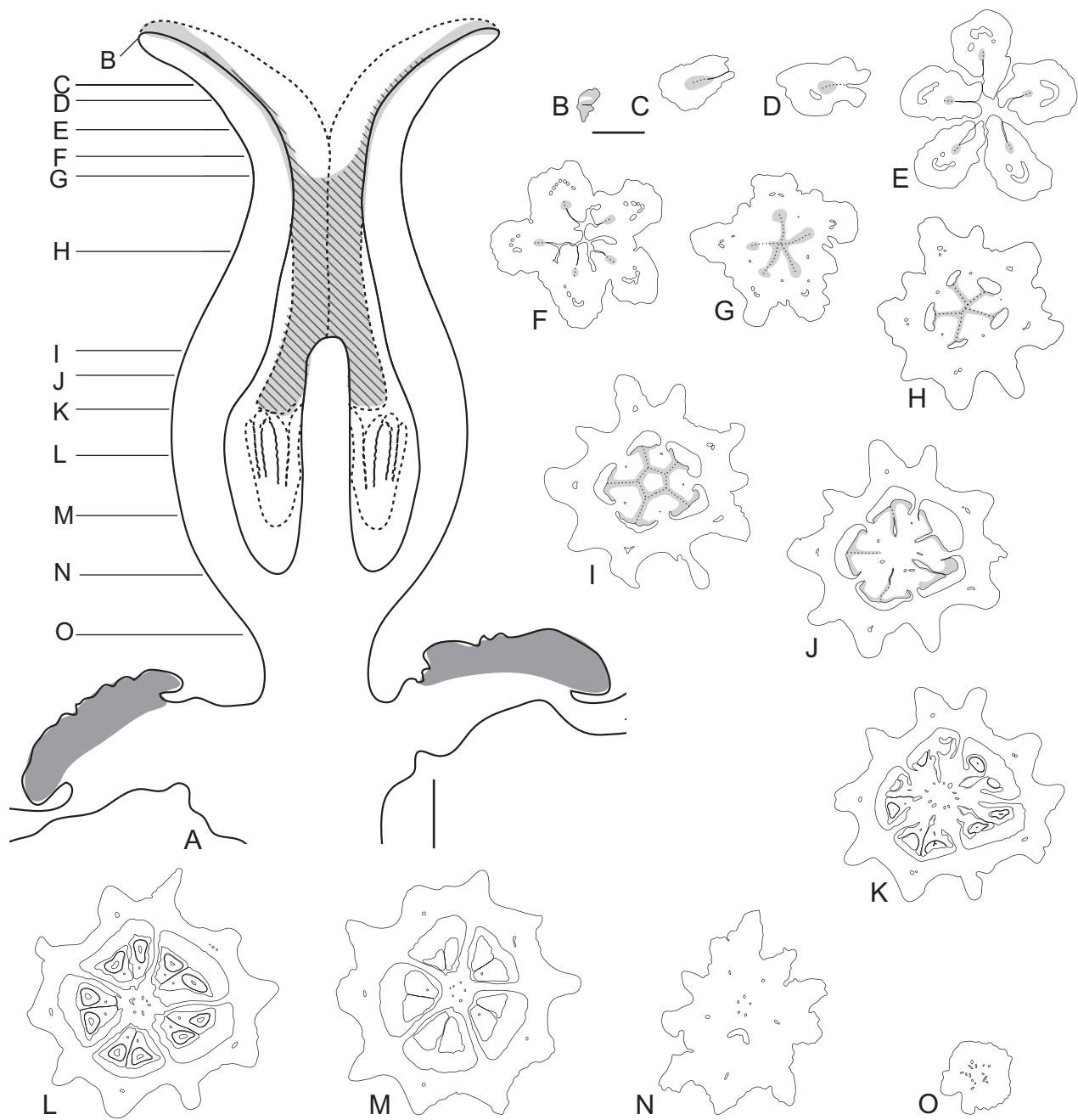
*Morphology:* Plants are ramiflorous, with flowers emerging in clusters. In some clusters, female flowers are present together with a single, centrally positioned, functionally male bud (morphologically bisexual); when females reach anthesis, the male bud is still closed (i.e. flower clusters appear to be protogynous). The functionally and also morphologically female flowers are small (see 'Flower size' in Glossary), polysymmetric and pentamerous (some with only four carpels) (Figs 1, 2, 63). Stamens are absent. Sepals and petals are much shorter than the gynoecium in bud and at anthesis, and do not form the protective organs in advanced buds (Figs 1, 19, 20, 31, 32). During and after anthesis, the ovary elongates substantially (Fig. 63). Some sepals may be shortly congenitally united, with irregular imbricate aestivation in the lowermost part of the free region, open above; they are not postgenitally connected. Sepals have a broad base and a pointed apex (Fig. 31). Petal aestivation is open (Fig. 1E). Carpels are antepetalous (Fig. 1D). The gynoecium is syncarpous up to the mid-style, free above; it is synascidiate up to above the placenta and is of angiospermy type 2 (Figs 1, 2). The elongate ovary is superior and has ten ribs: five median and five in between; those in between may be more prominent in the lower part of the ovary (Figs 1E, 63). A gynophore is present (Figs 1E–H, 2O). In bud, carpel tips are upright and contiguous (Figs 1A, 71); at anthesis, they reflex to expose the ventral stigmatic surfaces (Figs 2A, 63, 72). Stigmas are small and nonpapillate, decurrent on the ventral side (Figs 2B, 72); secretion appears to be absent at anthesis. Ventral slits extend up to the base of the stigma, where they are widely open (Fig. 72). In the plicate part of the style, ventral slits are closed along their inner angle and open at their flanks (Fig. 2C–E); in the upper symplicate zone, they are completely closed (Fig. 2F) and, in the lower symplicate zone of



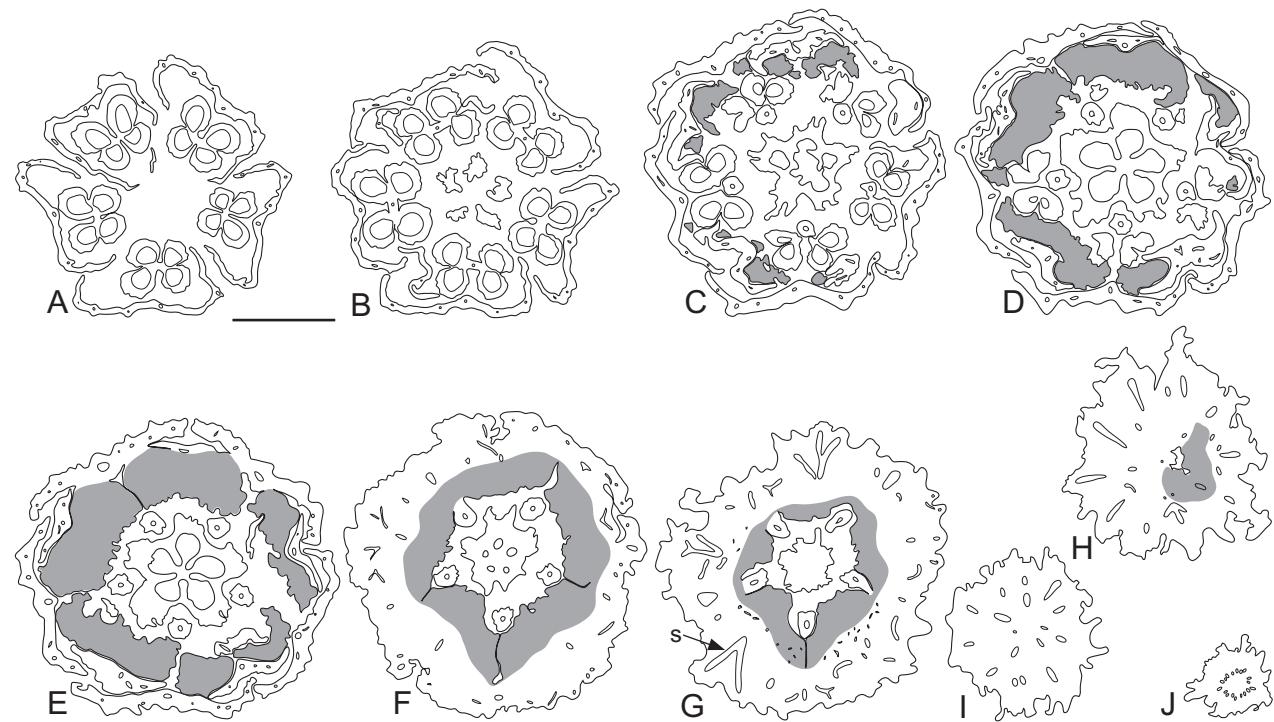
**Figure 1.** *Lophopyxis maingayi* (Lophopyxidaceae). Floral bud, morphologically female, transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines; nectary shaded grey. A, Level of free carpels with partially closed ventral slits. B, C, Level of symplicate zone of gynoecium; ventral slits postgenitally fused. B, Level of transition from style to ovary. C–E, Free petal parts with open aestivation. C, Transition of gynoecium from symplicate to synascidiate. D, Level of placenta. E–H, Level of antepetalous nectary lobes and gynophore. E, F, Level of petals; three of the five petals are incurved over the ovary, two are upright. F–H, Level of floral cup lined by nectary. H, Level of sepal and petal bundles joining. I, J, Floral base and pedicel. Scale bar, 500 µm.

the style and in the ovary, they are postgenitally fused (Figs 1B, C, 2G–I). They extend as postgenitally fused ventral furrows in the synascidiate zone (Fig. 2J). PTET is confined to the inner angle of the ventral slits as c. five cell layers in the plicate zone and uppermost part of the symplicate zone (Fig. 2A, C–F). Lower down in the symplicate zone the entire ventral slits are lined by a single cell layer of PTET, and a compitum is present (Fig. 2A, G–I). PTET extends into the locules along two nonpapillate obturators on the ventral side of each carpel (Fig. 2A, I, J). The transition zone from symplicate to synascidiate is noticeably elongate, which results in a ring-shaped compitum (in transverse section) (Fig. 2I). Obturators also span this zone between symplicate and synascidiate within the locule (Figs 2I, J, 83, 84). An apical septum is absent. Ovary septa are conspicuously thin at the level of the ovules (Fig. 2K–M). Placentation is axile at the locule mid-length, in the region in which the locule widens (above this region the locule is dorsoventrally narrow) (Figs 1D, 2A, K). Two collat-

eral, pendant antitropous ovules are present per carpel and the upper face of each ovule slopes downwards, towards the dorsal side of the carpel (the upper face is formed by the rim of the inner integument, which is shorter on the antiraphal side than on the raphal side) (Figs 2K, 83, 84). Ovules are anatropous, bitegmic and perhaps weakly crassinucellar; the nucellus is conspicuously long and slender (Fig. 109A). The upwards directed micropyle is formed by the longer inner integument (Figs 84, 96, 109A). The obturator comes into direct contact with the rim of the inner integument, but does not appear to protrude into it, although the obturator may extend downwards into the space between the integuments on the raphal side (Fig. 109A). The semiannular outer integument is three cell layers thick, the inner five or six cell layers. Both integuments are lobed. An endothelium is present (Fig. 109A). The nucellus disintegrates around the embryo sac. The antepetalous nectary lobes are large with a wrinkled surface; they surround the base of the gynoecium (Figs 1E–H, 38).



**Figure 2.** *Lophopyxis maingayi* (Lophopyxidaceae). Pentamerous gynoecium from female flower at anthesis; pollen tube transmitting tract (PTTT) shaded light grey. A, Schematic median longitudinal section with two carpels projected in the median plane. Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines; postgenitally fused areas are hatched; nectary shaded dark grey. B–O, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines. B–E, Plicate zone (B–D, one carpel drawn). B, Level of stigma. C–I, Level of postgenitally fused ventral slits. C–G, Level of style; PTTT confined to inner angle of ventral slits. C–F, Ventral slit postgenitally fused at inner angle and carpel flanks open. G–I, Level of compitum, entire ventral slits postgenitally fused. H–N, Level of ovary locules. I, J, Level of obturators. I, Transition from symplicate to synascidiate zone; level of ring-shaped compitum. J, Level of postgenitally fused internal ventral furrow. K–M, Level of collateral ovules. K, Level of placenta and micropyles; upper surface of ovules sloping downwards, away from ovule attachment. O, Gynophore. Scale bars, 200 µm.



**Figure 3.** *Lophopyxis maingayi* (Lophopyxidaceae). Floral bud, functionally male (morphologically bisexual) from male flower cluster, transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey; s, sepal synlateral. A–G, Level of antesepalous stamens. A–E, Free sepal parts (some sepals united in E). A–D, Level of anthers. B–G, Level of rudimentary gynoecium. B, Level of free carpels. C–H, Level of antepetalous nectary lobes. C–E, Free petal parts; level of symplicate zone of rudimentary gynoecium. C, Level of apical septum. E–H, Level of floral cup lined by nectary. F, G, Level of stamens joining floral cup. F, Level of synascidiate zone of rudimentary gynoecium. G, Level of lateral sepal bundles and petal bundles joining within the floral cup; level of gynophore. H, I, Level of stamen bundle joining median sepal trace. I, J, Floral base and pedicel. Scale bar, 500 µm.

Each lobe arises from the base of a petal and is supplied by a branch of the median vascular bundle of the petal (Figs 1E, F). Towards the floral base, petals and sepals unite into a floral cup, the inner surface of which is lined by the individual nectary lobes (Fig. 1F–H). The pedicel is not clearly articulated.

**Anatomy:** Sepals have one main and five or six secondary vascular bundles and three vascular traces (Fig. 1H). Petals have one (Fig. 1C) to three vascular bundles and one vascular trace. Median carpel vasculature extends up to below the stigma as a broad arch-shaped band of bundles (Fig. 2E); in the symplicate zone, it may separate into individual bundles, including main and secondary lateral carpel bundles, or remain as a single larger bundle (Fig. 2F). Small synlateral carpel bundles extend upwards into the base of the style (Fig. 2G, H); further proximally they branch and supply the ovules (Fig. 2K). The ovule bundle ends shortly before the chalaza; it does not branch (Fig. 109A). Below the placenta, synlaterals

form a ring in the centre of the gynoecium; they join the median carpel bundles in the gynophore (Fig. 1H). In the floral cup, petal bundles join the lateral sepal traces (Fig. 1H) and these bundle complexes with the sepal traces join the gynoecial bundles in the pedicel to form a central stele.

**Histology:** Unicellular, lignified hairs are present on both sepal surfaces (dense on the dorsal side), the dorsal side of the petals, and densely cover the gynoecium (Figs 31, 32). Tanniferous tissue is abundant in all floral organs. Cells with oxalate druses are also present in all floral organs; they are especially abundant in the ovary septa, lining either side of the ventral slits in the symplicate zone, and in the centre of the gynoecium. Sclerenchyma, mucilage cells and special mucilage cells (see Glossary) are absent.

*Lophopyxis maingayi* (*male*)  
Figures 3, 25, 29, 30, 39, 48, 56.

**Morphology:** Plants are ramiflorous with flowers emerging in clusters of c. seven to nine purely male flowers or singly with a few female flowers (see description above for female flowers). Flowers are functionally male, but morphologically bisexual (Fig. 3). They are small, polysymmetric, pentamerous and haplostemonous (stamens antesepalous). In contrast with the female flowers, sepals form the protective organs still in advanced buds (Fig. 25) and each sepal enwraps a stamen in bud (Fig. 3A). Sepals are involute-valvate near the apex (Fig. 3A), with irregular imbricate aestivation lower down (Fig. 3E) (in male flowers from the female flower cluster the sepals may be shortly congenitally united); sepals are not postgenitally connected. Sepals have a broad base and a pointed apex; the pointed tips are curved into the centre of the bud. Petals are much shorter than the sepals still at anthesis (Fig. 3C–E); their aestivation is open (Fig. 3C, D). Petals have a broad blade and a narrow attachment region (Fig. 3E). Stamen maturation and dehiscence appear to be staggered, whereby the filaments of neighbouring stamens elongate and the anthers dehisce whilst others remain short and the anthers closed (with the sepal apex still curved over the top of the stamen) (Figs 29, 30). Filaments are longer than anthers at anthesis. Anthers are 'X'-shaped, basifix, latrorse (extrorse towards the theca base) and nonversatile (Figs 48, 56). The connective is relatively broad and thin; a protrusion is absent. Thecae dehisce via longitudinal slits, which are not continuous over the anther apex. Endothecium is not continuous over the connective or on the inner side of each theca. A rudimentary gynoecium with antepetalous carpels is present (Figs 3B–G, 29, 30, 39). It is syncarpous in the superior ovary (Fig. 3C, F) and is elevated on a gynophore (Fig. 3G). The ovary is synascidiate only in its lowermost part (Fig. 3F). Up to three ribs are present on the outer wall of each carpel (Fig. 3C). The apocarpous parts of the gynoecium are solid (Fig. 3B). In the syncarpous ovary, carpels have widely open ventral slits (incomplete angiospermy) and the 'inner' morphological surface is exposed. Only in some carpels is a postgenitally fused ventral slit present in the upper part of the ovary. Stigmas, placenta, ovules and PTTT are absent. The five antepetalous nectary lobes are large with a wrinkled surface and surround the rudimentary ovary (Fig. 39); they arise from the base of the petals (Fig. 3E). Towards the floral base, petals and sepals unite into a floral cup whose inner surface is lined by the individual nectary lobes (Fig. 3E–H). Stamens join the floral cup towards its base (Figs 3F, G). The concave centre of the floral base is also nectariferous (Fig. 3H). The pedicel is not clearly articulated.

**Anatomy:** Sepals have three main and c. four secondary vascular bundles and three vascular traces (Fig. 3G). Petals have three to five vascular bundles and a single vascular trace (Fig. 3F). Stamens have a single vascular bundle. Nectary lobes are supplied by scattered phloematic bundles diverging from the petal bundle in the nectary base (Fig. 3G). In the floral cup, the petal bundles join the closest lateral sepal bundles (Fig. 3G). Vasculature is mostly absent from the rudimentary gynoecium, except for a single small bundle in the base of the gynophore (Fig. 3H). In the pedicel, stamen vascular bundles join the other bundles to form a central stele.

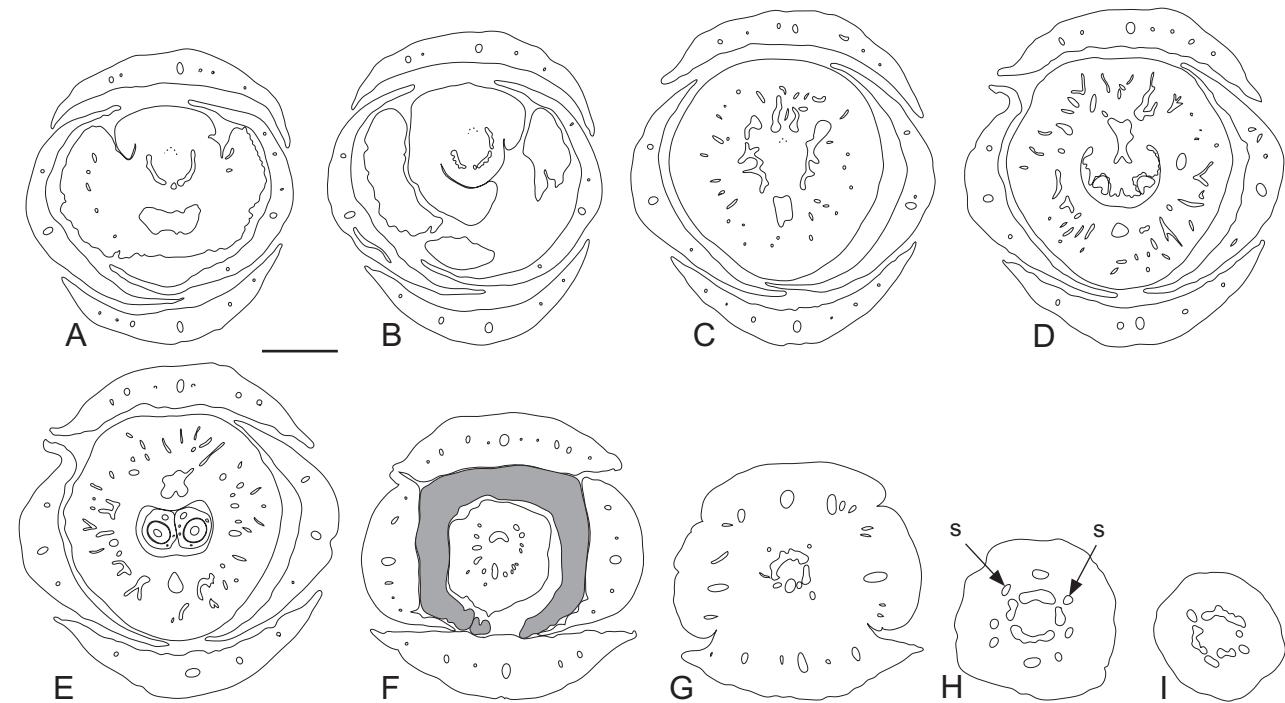
**Histology:** Unicellular, lignified hairs are present on both sides of the sepals and petals, on the stamen filaments and covering the rudimentary gynoecium, even within the ovary locules. Stomata are present on the dorsal side of the sepals and on the nectary lobes. Abundant tanniferous tissue and cells with oxalate druses are present in all floral organs; in the anther, oxalate druses are concentrated in the connective and are also present in the nectary lobes. Cells with raphides line the walls of the pollen sacs. Sclerenchyma, mucilage cells and special mucilage cells are absent.

#### PUTRANJIVACEAE

*Drypetes deplanchei* (*female*)

Figures 4, 5, 68, 78, 79, 95, 103, 104, 109B.

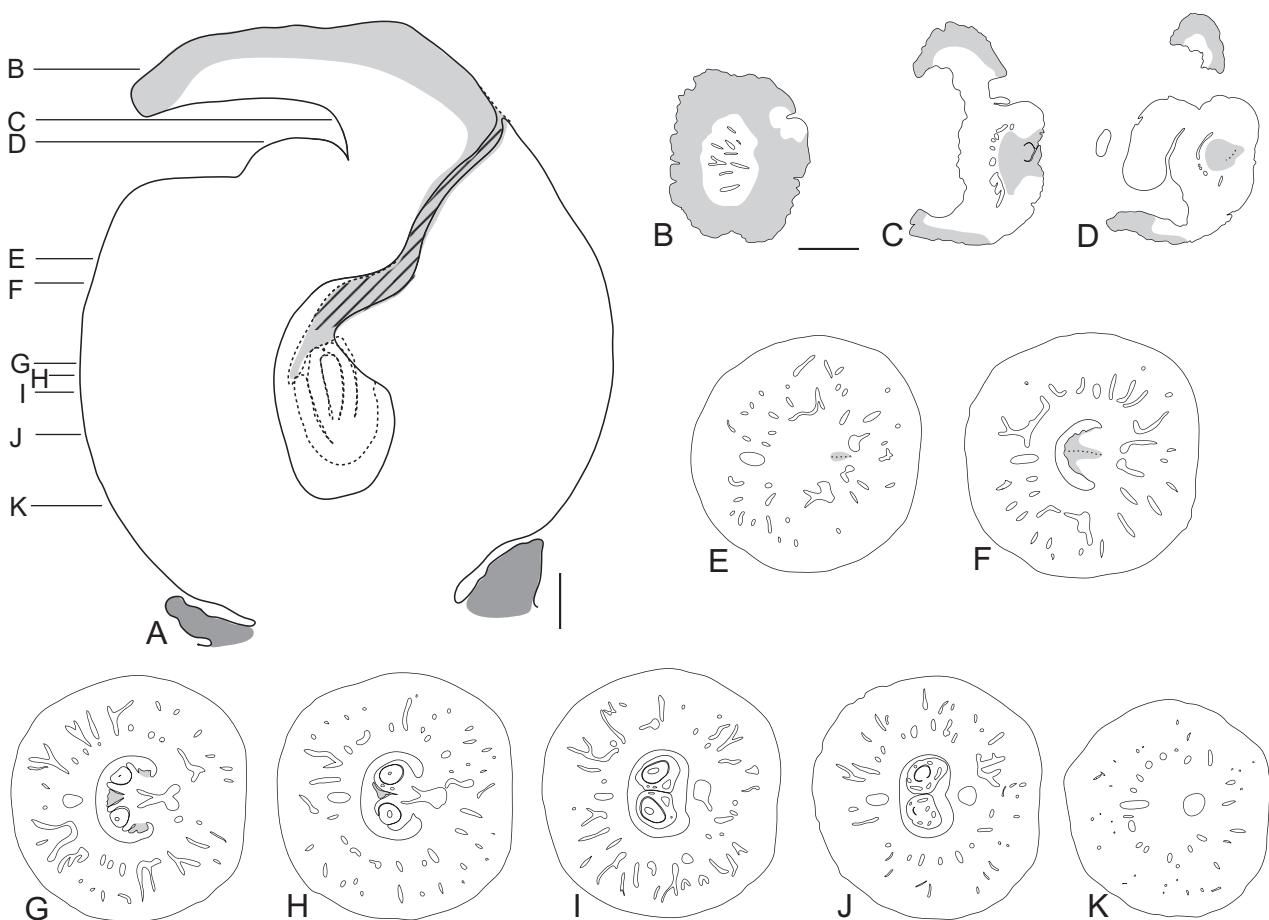
**Morphology:** The detailed description is based on a flower with a single (fertile) carpel; observations of the two-carpellate gynoecium are based on SEM and dissecting microscope studies. Flowers are functionally and morphologically female. They are small and polysymmetric, with four sepals (or five sepals, the innermost sepal appearing petal-like) and one (or more rarely two) fertile carpels (Figs 4, 5, 68, 78, 79). Petals and stamens are absent. Sepals have a decussate arrangement (Fig. 4) when four sepals are present (quincuncial when five sepals are present) and still form the protective organs in advanced buds, but are not postgenitally connected. Sepals are widely open at anthesis and abscise after anthesis. The inner sepals have a narrower base than the outer ones (Fig. 4F). Individual sepals have a broad base and a rounded apex; some may be shortly congenitally united (Fig. 4F). The gynoecium is of angiospermy type 2; it is ascidiate up to the lower part of the style (Fig. 5A, D–J), plicate above (Fig. 5A–C). The superior ovary is globular (Fig. 68). Its upper dorsal and lateral parts are misshapen by an imprint corresponding to a depression left by the stigma in the bud phase (Fig. 5A). The almost sessile stigma is reflexed



**Figure 4.** *Drypetes deplanchei* (Putranjivaceae). Floral bud, morphologically female, transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines; nectary shaded grey; s, sepal synlateral. A–F, Free sepal parts (in F, two sepals united); level of gynoecium. A, B, Level of crescent-shaped stigmatic branch. B, Level of styilar base and beginning of ovary. D, E, Level of ovules. D, Level of placenta and obturator. F, Level of gynophore and nectary. G–I, Floral base and pedicel. Scale bar, 500 µm.

exposing the large receptive surface (in the dimerous gynoecia stigmas are smaller, the gynoecium syncarpous up to the base of the stigma) (Figs 5A, 78, 79). The large crescent-shaped stigma is dorsoventrally flattened with an undulating margin and a narrower base (Fig. 4A); it is nonpapillate and secretion appears to be present at anthesis. A gynophore is present (Figs 4F, 5K). A ventral slit extends up to the base of the stigma where it is widely open (Figs 5A, 79); lower down in the style it is closed (Fig. 5C); it is postgenitally fused directly above and within the ascidiate zone, where it is present as an inner slit (Figs 4A–C, 5D–F). A styilar canal is absent. Circa ten cell layers of PTTT form the receptive surface of the stigma with c. 10–15 cell layers lining the ventral slit in the style. PTTT diminishes to three to five cell layers at the flanks of the slits above the ascidiate zone and c. ten cell layers at the inner angle of the slit. In the upper part of the ascidiate zone, the ventral furrow is lined by c. four to ten cell layers of PTTT, which extend into the locule as c. five cell layers lining the ventral furrow and the papillate obturators. Placentation is apical and axile (Fig. 5G, H). Two collateral, pendant antitropous ovules are

present: the upper face of each ovule slopes downwards, towards the dorsal side of the carpel (Figs 5G, H, 95). Ovules are bitegmic, anatropous and perhaps weakly crassinucellar; the nucellus is long and slender (Fig. 109B). The upwards directed transverse slit-like micropyle is formed by the longer inner integument (Figs 103, 104, 109B). The obturator is in direct contact with the rim of the inner integument and may also protrude into it in ovules with a more open micropyle (it does not come into contact with the nucellus); the obturator also extends downwards into the space between the integuments on the raphal side (Fig. 109B). Both integuments are lobed; however, the lobes of the outer integument are mostly confined to the antiraphal side, and may result in a median slit in the rim. At its base, the inner integument begins higher up on the raphal side than on the antiraphal side (Figs 5J, 109B). The semiannular outer integument is three or four cell layers thick and the inner integument is five to seven cell layers thick. An endothelium is only weakly differentiated (Fig. 109B). The nucellus disintegrates around the embryo sac. A short cup-like nectary with an uneven rim surrounds the base of the gynoecium (Fig. 4F). At the shallowly

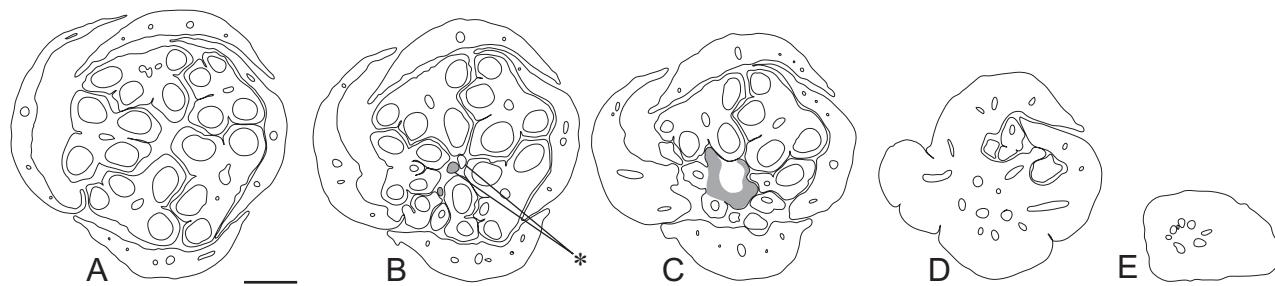


**Figure 5.** *Drypetes deplanchei* (Putranjivaceae). Monocarpellate (pseudomonomerous?) gynoecium from female flower at anthesis; pollen tube transmitting tract (PTTT) shaded light grey. A, Schematic median longitudinal section (dorsal side left). Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines; postgenitally fused areas are hatched; nectary shaded dark grey. B–K, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines. B–D, Level of stigma. B, C, Level of plicate zone. D–J, Level of ascidiate ovary. D–F, Level of postgenitally fused internal ventral furrow. F–H, Level of obturators. G–J, Level of collateral ovules. G, H, Level of placenta; upper face of ovules sloping downwards, away from ovule attachment. H–J, Level of vasculature in outer integument of ovules. J, Level of inner integument beginning higher up on the raphal than the antiraphal side. K, Ovary base. Scale bars, 200 µm.

concave floral base, the nectary sits at about the same level as the inner sepals and ovary. The pedicel is not obviously articulated.

**Anatomy:** Sepals have three main and two to four secondary vascular bundles and three vascular traces (the laterals forming synlaterals) (Fig. 4G, H). A band of vasculature (including a dorsal bundle) extends into the stigma and forms a semicircle of bundles around the dorsal side of the lower part of the stigma and short style (Figs 4A, B, 5C, D); in the ovary, these bundles are joined by numerous additional lateral bundles, which anastomose with each other and completely surround the strand of PTTT. A large ventral

bundle extends upwards from the gynophore into the placenta (Figs 4D–F, 5H–K); it divides and supplies the ovules (Figs 4D, 5G, H). Branches from the ventral bundle also extend above the placenta into the upper part of the ovary wall (Figs 4C, 5E, F). The ovule bundle extends to the chalaza; it branches from the chalaza and also from the lower part of the raphe into the outer integument (Figs 5I, J, 109B). Below the locule, secondary lateral bundles join and also unite with the main dorsal or ventral bundles. In the centre of the gynophore and floral base, they form a ring of bundles, together with the dorsal and ventral bundle complexes (Fig. 4F). Numerous small phloematic bundles branch from the gynoecial bundles



**Figure 6.** *Drypetes deplanchei* (Putranjivaceae). Floral bud, functionally male (morphologically bisexual), transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey. A–C, Free sepal parts; level of stamens. B, C, Level of nectary. B, Level of rudimentary gynoecium (lines with asterisk). C–E, Floral base and pedicel. C, Level of stamens joining convex floral base. Scale bar, 500 µm.

into the base of the nectary. Bundle complexes join to form a central stele in the pedicel.

**Histology:** Uniseriate, two- or three-cellular, lignified hairs are present on the dorsal side near the apex and margins of the sepals, and are scarce on the ventral side; they are also present on the pedicel (hairs tanniferous) and ovary. Tanniferous tissue is present in the sepals and is abundant in the ovary. Cells with oxalate druses are present in the sepals, ovary and nectary. Stomata (not raised) are present on the dorsal sepal surface and also on the dorsal surface of the stigmatic branches; they were not observed on the nectary. Laterally positioned patches of sclerenchyma are present in the stigma and form a band on the ventral side of the style in the ascidiate zone. Mucilage cells and special mucilage cells are absent.

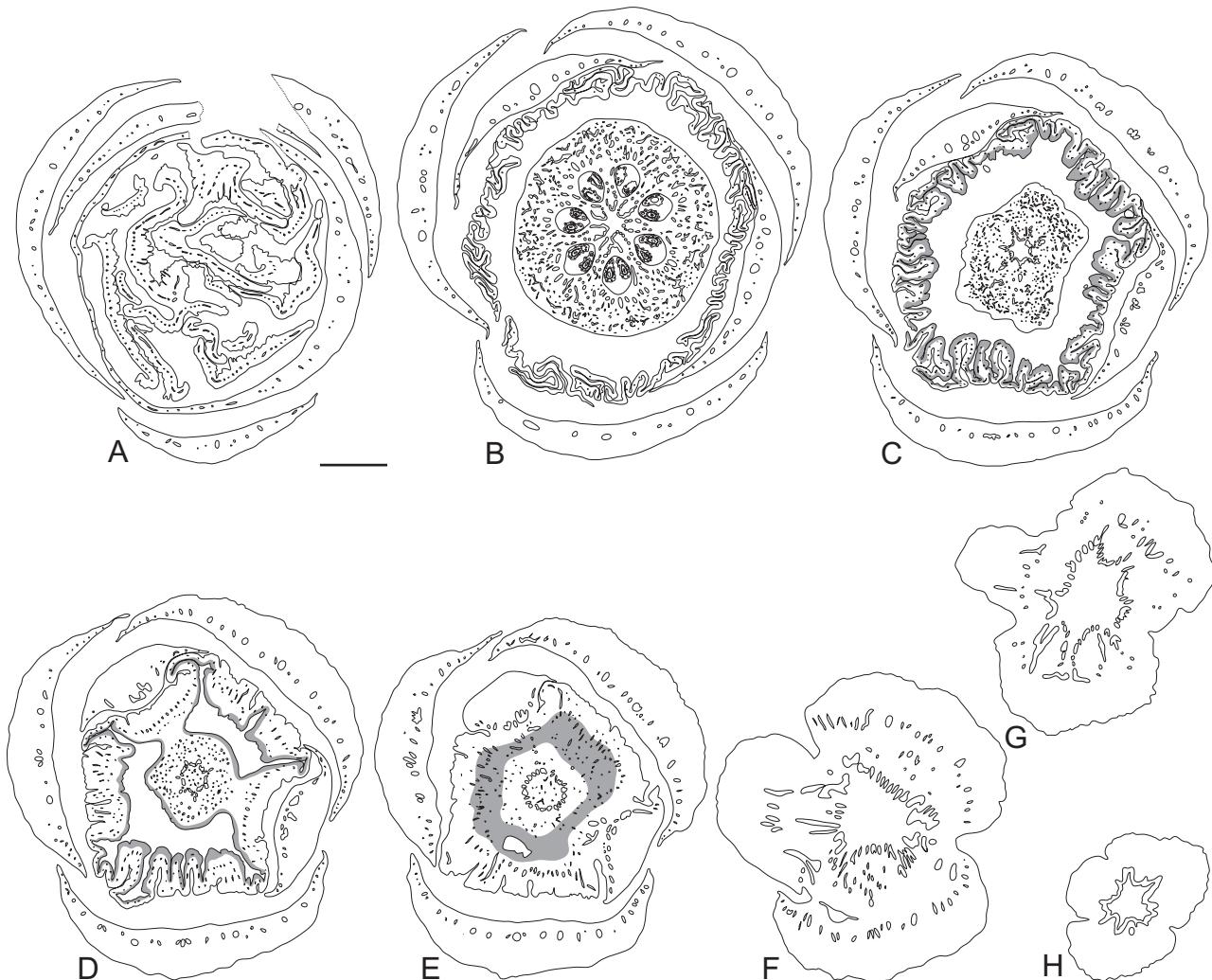
#### *Drypetes deplanchei (male)* Figures 6, 46, 52, 60.

**Morphology:** Flowers are functionally male, but morphologically bisexual (Fig. 6). They are small and polysymmetric with four (or five) sepals and (five–) seven (–eight) stamens (diplostemonous when four sepals and eight stamens are present). Petals are absent. One or two solid rudimentary carpel(s) may be present (Figs 6B, 46). Sepals form the protective organs still in advanced buds; they are widely open at anthesis. Some sepals may be shortly congenitally united; they are imbricate in their free parts, but are not postgenitally connected. The inner sepals are broader and longer than the outermost one. Sepals have a broad base and a rounded apex with ciliate margins. In flowers with seven stamens, three stamens are antesepalous in the radii of the three outer sepals, the other stamens alternate with the sepals. All stamens are of similar length. Filaments are shorter than anthers still at anthesis. Anthers are

irregularly shaped and of varying sizes, but overall they are 'X'-shaped, introrse, basifixated into a pseudopit and nonversatile (Figs 52, 60). The connective is broad and thick; a protrusion is absent. Thecae dehisce via longitudinal slits, which are not continuous over the anther apex. An endothecium was not apparent in the bud stage studied. The floral centre is nectariferous and extends as a dorsoventrally flattened rim over the bases of the stamen filaments (Fig. 46). In flowers with rudimentary carpels, the lower part of the carpels may also be nectariferous (Fig. 6B). The floral base is shallowly convex. The pedicel is weakly articulated at the base.

**Anatomy:** Sepals have one to three main and one or two secondary vascular bundles and three vascular traces (Fig. 6D). Stamens have a single vascular bundle (which may appear collaterally doubled within the anther; Fig. 6A). A short bundle extends into the base of the rudimentary carpels. The nectary is vascularized by small phloematic bundles, which extend from the single gynoecial bundle in the floral base. In the floral base, adjacent stamen bundles may join. Stamen vascular bundles unite with sepal traces and, together with the gynoecial/nectary bundle complexes, they form a central stele in the pedicel.

**Histology:** Uniseriate, two- or three-cellular, lignified, tanniferous hairs are present on both sepal surfaces and especially along their margins and on the pedicel; those on the anthers (hairs may be branched) (Figs 52, 60) and those on the upper surface of the nectary are unlignified. Tanniferous tissue is scarce but, when present, is generally associated with the vascular bundles of the sepals and is also present in the pollen and nectary. Cells with oxalate druses are also scarce in the sepals and anthers. Stomata are present on the dorsal side of the sepals. Sclerenchyma, mucilage cells and special mucilage cells are absent.



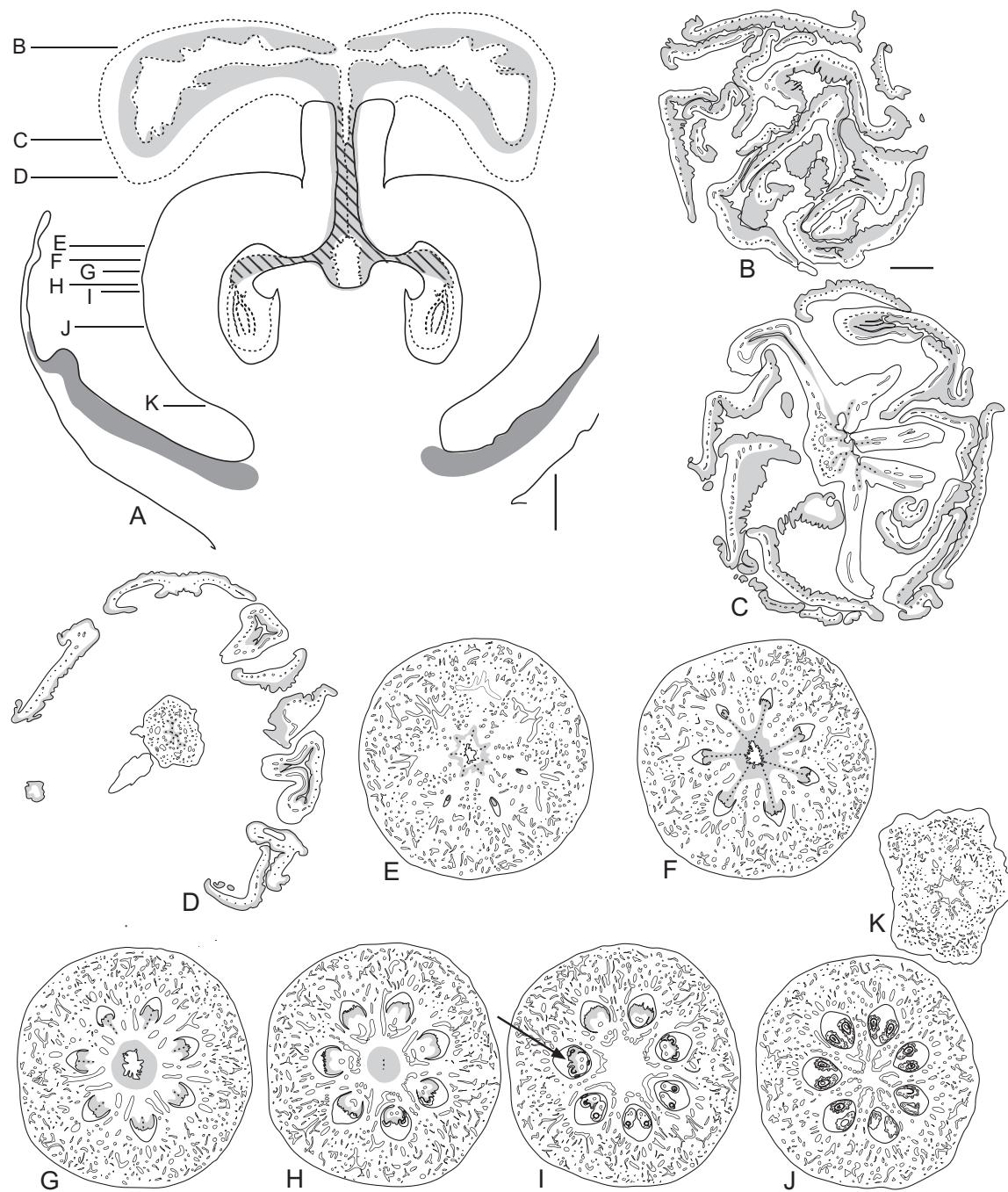
**Figure 7.** *Drypetes gossweileri* (Putranjivaceae). Flower after anthesis (sepals closed again), morphologically female, transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; nectary shaded grey. A–E, Free sepal parts (in A, one sepal damaged by herbivores; in E, inner sepals joining floral base). A–C, Level of seven-carpellate gynoecium. A, Level of stigmas. B–E, Level of nectary (in B–D, nectary sinuously curved). B, Level of ovary with collateral ovules. C, Level of gynophore. D, Level of nectary uniting with gynophore at convex floral base; gynophore also nectariferous at this level. E–H, Floral base and pedicel. Scale bar, 2 mm.

#### *Drypetes gossweileri (female)*

Figures 7, 8, 41, 75, 76, 89–91, 107, 108, 109C.

**Morphology:** The detailed description is based on serial sections of flowers after anthesis, including that of the gynoecium, and SEM studies of an anthetic gynoecium. Flowers are functionally and also morphologically female (Fig. 7). They are medium sized (*c.* 8 mm) and polysymmetric with five sepals and seven carpels (Figs 7, 8); petals and stamens are absent. Sepals are reflexed at anthesis, but close again after anthesis and give the superficial appearance of a floral bud. Sepal aestivation is quincuncial; the outer two sepals are much shorter than the inner three,

which cover the apex of the bud; they are not postgenitally connected. Sepals are thick and leathery with fringed margins, a broad base and a narrow, rounded apex. The gynoecium is syncarpous up to the lower style (Fig. 8A); it is of angiospermy type 4. The superior, globular ovary is elevated on a short gynophore (Figs 7C, 8K); the stylar region is short, and seven large, reflexed, dorsoventrally flattened non-papillate stigmas with many short lobes and a ridged ventral surface are present (Figs 7A, 8B–D, 75, 76). Stigmatic secretion appears to be present at anthesis. Although the ovary is synascidiate up to above the placenta, the transition zone from symplicate to synascidiate is long and is concave rather than convex



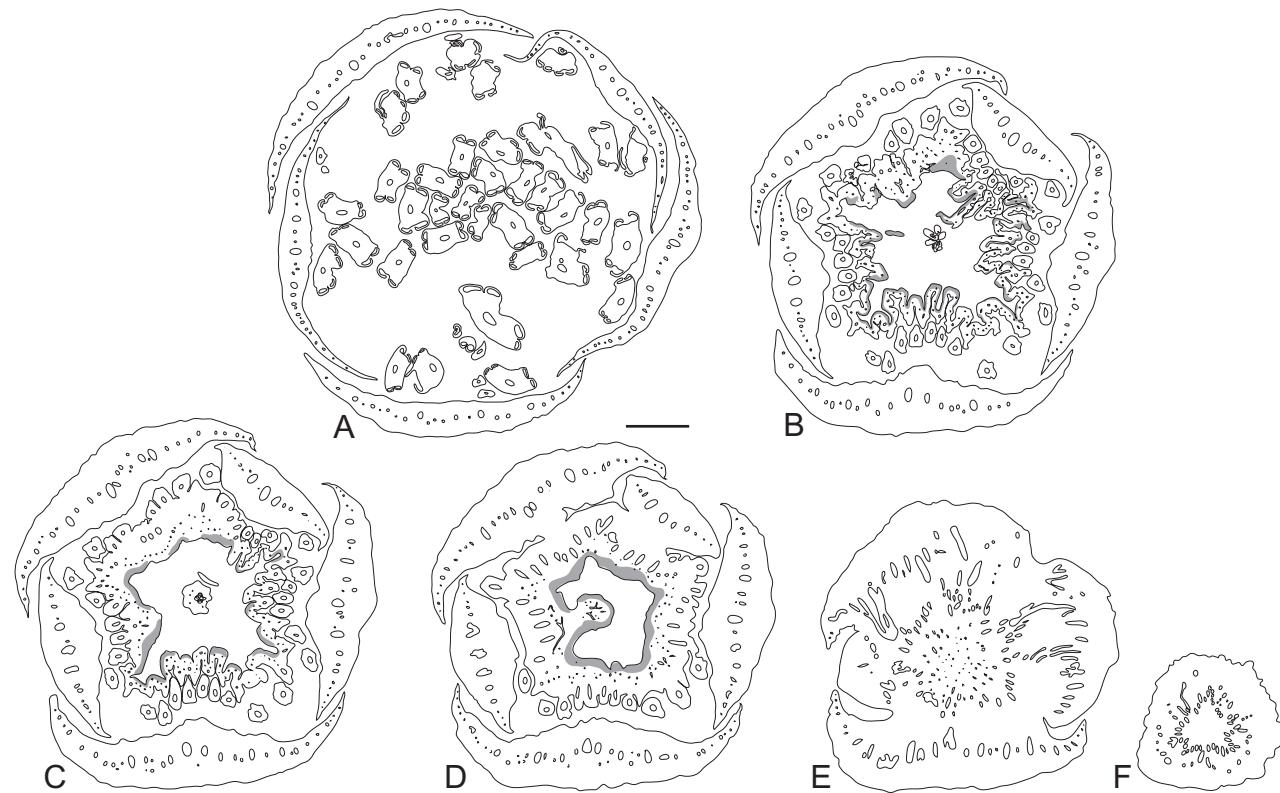
**Figure 8.** *Drypetes gossweileri* (Putranjivaceae). Gynoecium of female flower after anthesis; pollen tube transmitting tract (PTTT) shaded light grey. A, Schematic median longitudinal section. Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines; postgenitally fused areas are hatched; nectary shaded dark grey. B–K, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines. B–D, Level of free stigmatic branches. C–H, Level of compitum. C–F, Level of symplicate zone with postgenitally fused ventral slits. C, D, Level of style. E–J, Level of ovary locules. D, Level of stylar base. E–G, Level of hole in centre of gynoecium lined by papillate PTTT. E, Level of apical septum. F–I, Level of papillate obturators. G, H, Transition from symplicate to synascidiate zone. H–J, Level of collateral ovules. H, I, Level of downwards protruding placentae; level of micropyles (arrow points to a pair of ovules facing each other). J, Level of ovules with numerous vascular bundles in outer integument. K, Gynophore. Scale bars, 1 mm.

(Fig. 8A, G). As a consequence, a central hole (as seen in transverse sections) is present in the septate ovary (Fig. 8E–G). A postgenitally fused ventral slit extends up to below the stigmatic branches and throughout the symplicate zone (Fig. 8A, C–F). In the upper part of the synascidiate zone, it is present as an internal postgenitally fused ventral furrow (Fig. 8G), which is shallow at the placenta. PTTT is present as four to seven cell layers on the ventral side of the stigma, and two or three cell layers line the ventral slit in the style and symplicate zone of the ovary, and also the ventral furrow in the synascidiate zone. The central hole is lined by multicellular papillate PTTT. It forms part of the compitum, which extends throughout the symplicate zone (Fig. 8E–G). PTTT also forms the floor of the hole (Fig. 8H). An apical septum is present (Fig. 8E). Two large obturators with long multicellular papillae span the symplicate and synascidiate zones within the locule above the placenta (Figs 8F–I, 89–91). In each carpel, the obturators surround the upper part of the two ovules (Figs 91, 109C). Placentation is axile and the placenta hangs downwards into the locule (Fig. 8A, H, I). Two pendant collateral, antitropous ovules are present per carpel (Figs 8H–J, 89, 109C). Within a locule, the upper face of each ovule slopes downwards towards the neighbouring ovule (Fig. 8I). The laterally flattened ovules are bitegmic and anatropous; the nucellus is long and slender (Fig. 109C). A gap is present between the integuments, especially in the lower part of the ovule (Figs 107, 108, 109C). The rim of the outer integument protrudes above that of the shorter inner integument, but does not take part in micropyle formation as its entrance is widely open (Figs 107, 108, 109C). Instead, the upwards facing, transverse slit-like micropyle is formed by the inner integument alone (Fig. 108). The rims of both integuments are in close contact with the obturator, and the obturator protrudes downwards between the integuments; it does not, however, protrude directly into the micropyle (Figs 91, 109C). At their base, the inner integument and nucellus begin higher up on the raphal side of the ovule than on the antiraphal side (Figs 8J, 109C). Both integuments are lobed; the two lobes of the outer integument form a shallow lateral slit, whereby lateral slits of the adjacent ovules within a carpel face each other (Fig. 8I). Both integuments are five or six cell layers thick, the outer integument is semi-annular. Ovules have a thickened raphe; their surface is ridged by the presence of vasculature in the outer integument (Fig. 107). An endothelium is present. The nucellus disintegrates around the large embryo sac already in bud. The gynoecium base is surrounded by a dorsoventrally flattened, cup-shaped, strongly sinuous nectary disc (Figs 7B–D, 41). The disc is thickened at the base in antesepalous sectors

and appears to be nectariferous on its inner surface (Fig. 7C, D). Its upper parts lack cells with deeply staining cytoplasm and are probably not secretory. The nectariferous zone also involves the base of the gynophore (Fig. 7D). The floral base is convex. The pedicel is not obviously articulated.

**Anatomy:** Sepals have four to six main and c. 30–40 secondary vascular bundles, and c. three vascular traces in the inner three sepals, c. five in the outer two sepals (Fig. 7E–G). A broad band of bundles extends into each stigmatic branch, formed by a dorsal and four primary plus secondary lateral bundles. Numerous additional lateral bundles are present in the ovary wall and form a dense network with each other and with the dorsal and primary lateral carpel bundles (Fig. 8E–J). In the synascidiate zone, the primary lateral carpel bundles closest to the gynoecium centre join to form ventral bundles which divide to supply the ovules. The ovule bundle branches from the raphe and from the chalaza into the outer integument (Figs 8J, 109C). Below the level of the placenta, each ventral bundle complex forms a broad crescent-shaped band of bundles (Fig. 8I); these bands of bundles divide lower down and join with neighbouring carpel bundles to form synlaterals between the carpels (Fig. 8J). Towards the locule base, these bundles form a star-shaped ring in the centre of the gynoecium (Fig. 8K). The dorsal carpel bundles join this ring at the level of the gynophore together with the numerous secondary carpel bundles. Small vascular bundles (phloematic bundles in their upper parts) originating from the gynoecial bundles in the floral base extend into the base of the nectary (Fig. 7B–E). Sepal traces and the gynoecial/nectary bundle complexes join and a central stele is formed in the pedicel.

**Histology:** Uniseriate, three- to nine-cellular lignified and unlignified hairs are present on both sepal surfaces (dense on the dorsal side, hairs are lignified especially where the sepal surface is exposed in bud), on the dorsal side of the stigmatic branches, on the style and ovary (Fig. 76), also continuing onto the nectary surface closest to the gynoecium and also at the base of the nectary lobes on their dorsal side (Fig. 41). Cells with oxalate druses are present in the sepals, gynoecium (including ovules) and nectary disc. Tanniferous tissue is not abundant but, when present, is concentrated around the vasculature of the sepals and gynoecium; it is also present in the nectary and in the epidermis of the ventral surface of the stigma. Raised stomata are present on the dorsal sepal surface and on the ovary. Sclerenchyma, mucilage cells and special mucilage cells are absent.



**Figure 9.** *Drypetes gossweileri* (Putranjivaceae). Floral bud, functionally male (morphologically bisexual), transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey. A–D, Free sepal parts (in D, inner sepals joining nectary); level of stamens. A, Level of anthers. B–D, Level of nectary (nectary sinuously curved in B and C). B, C, Level of rudimentary gynoecium. B, Level of free carpels. C, D, Level of stamens and nectary becoming confluent. C, Level of symplicate zone of rudimentary gynoecium. D, Level of nectary joining gynophore of rudimentary gynoecium. E, F, Floral base and pedicel. Scale bar, 3 mm.

#### *Drypetes gossweileri (male)*

Figure 9.

**Morphology:** Flowers are functionally male, but morphologically bisexual (Fig. 9). They are medium sized, polysymmetric with five sepals and c. 40 stamens. Petals are absent. A rudimentary gynoecium with six carpels is present (Fig. 9B, C). Sepals form the protective organs still in advanced buds; at anthesis, they are reflexed. Sepal aestivation is quincuncial; the two outer sepals are shorter and broader than the three inner ones; postgenital connection between the sepals is absent. Sepals are thick and leathery with a broad base, a rounded apex and fringed margins. Stamens are in a single series (Fig. 9C) with alterni-sepalous stamens either in single positions or in pairs (Fig. 9C, D). Filaments are longer than anthers at anthesis. At anthesis, the anther flips backwards (bending at the narrow joint between the anther and filament) to expose the ventral side of the anthers.

Anthers are elongate, 'X'-shaped, dorsifixed close to the base and latrorse (to introrse in their lower part). The connective is conspicuously thick and broad (the pollen sacs narrow and thin in comparison) (Fig. 9A); a protrusion is absent. Anther dehiscence is via two longitudinal slits, which are not continuous over the anther apex. The endothecium is continuous over the ventral side of the connective in the lower part of the anther; it is not continuous behind the thecae. Some neighbouring stamen filaments are fused at their base (Fig. 9B). The carpels of the rudimentary gynoecium are free in their upper parts (Fig. 9B), syncarpous below (Fig. 9C). Some carpels are solid in their upper parts, whereas others have an open ventral slit, which, in some carpels, extends up to below the apex. The superior ovary is unilocular and contains rudimentary ovules. A gynophore is present (Fig. 9D). A dorsoventrally flattened, cup-shaped, sinuously curved nectary with a secretory inner surface is present surrounding the rudimentary

carpels (Fig. 9B). It fuses with the stamens above the floral base (the antesepalous stamens mostly joining the nectary above the alternisepalous ones) (Fig. 9C, D). The floral base is convex.

**Anatomy:** Sepals have c. three to six main and c. 10–30 secondary vascular bundles and three to six vascular traces (Fig. 9E). Stamens have a single vascular bundle. Numerous small vascular bundles originating in the floral base extend into the sinuous nectary lobes. Small vascular bundles extend from below into the syncarpous part of the gynoecium, with neighbouring bundles joining in the gynophore (Fig. 9C, D). At the floral base, the gynoecium bundles and stamen/nectary bundles form bundle complexes and lateral sepal traces form synlaterals. These bundle complexes join the closest sepal trace and, together with the remaining bundles, form a central stele in the pedicel.

**Histology:** Uniseriate, multicellular (three to six cells) lignified and unlignified hairs are dense on both sepal surfaces. Stomata are present on the dorsal sepal surface, and dorsal side of the anthers (some stomata raised). Cells with oxalate druses are present in the sepals, stamens and nectary. Tanniferous tissue is present, but not abundant, in the sepals and nectary; when present, it is concentrated around the vascular bundles; it is also present in the filaments and anthers, concentrated behind the thecae, and in the rudimentary gynoecium. Sclerenchyma, mucilage cells and special mucilage cells are absent.

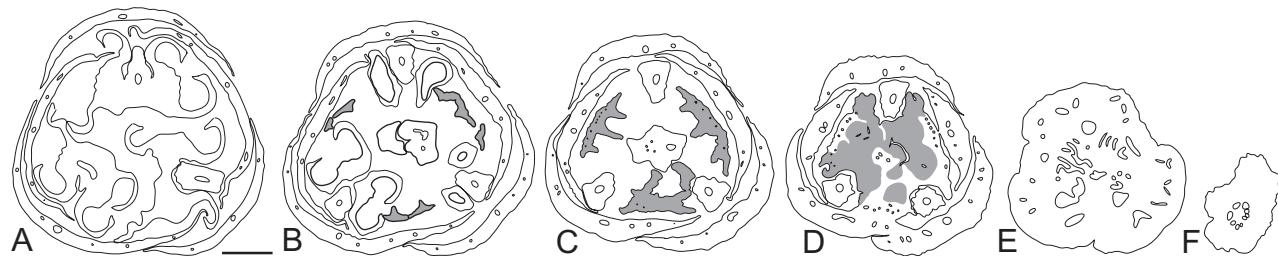
#### *Drypetes madagascariensis (female)*

Figures 27, 65, 66, 80, 94.

**Morphology:** The description of the upper part of the gynoecium is based on floral buds, as no anthetic flowers with an entire gynoecium with both styles intact were available. Flowers are functionally and also morphologically female; they are small and polysymmetric, with five sepals and two carpels (one carpel appears to be on the radius of the outermost sepal); petals and stamens are absent (Fig. 66). Sepals form the protective organs still in advanced buds (Fig. 27). Sepal aestivation is quincuncial; the two outer sepals are narrower and shorter than the inner three; they are not postgenitally connected. Sepals are thin and have a broad base, rounded apex and fringed margins. The gynoecium is syncarpous up to the lower part of the relatively long style (in comparison with other taxa with almost sessile stigmas) (Fig. 66); it is of angiospermy type 4. The free parts of the gynoecium are reflexed in open flowers (Fig. 66) (bent to one side of the gynoecium in bud and causing indents in the ovary wall tissue;

Fig. 65). The ovary is superior with an extremely short gynophore; it is synascidiate up to above the placenta. The large, dorsoventrally flattened stigmatic branches have a nonpapillate receptive surface (Fig. 80). A mostly closed ventral slit extends up to below the stigma; in the symplicate zone, it is postgenitally fused and, in the synascidiate zone, it is present as an internal ventral furrow. PTTT lines the ventral slit as two or three cell layers in the symplicate part of the style, and c. five cell layers lining the slit in the symplicate and synascidiate zones of the ovary. A compitum is present throughout the symplicate zone. The prominent obturators span between the symplicate and synascidiate zones just above the placenta (Fig. 94). Placentation is apical and axile. Two collateral, pendant antitropous ovules are present per carpel (Fig. 94); the upper face of each ovule slopes downwards towards the dorsal side of the carpel. Ovules are bitegmic and anatropous; the nucellus is long and slender. The upwards directed micropyle is formed by the longer inner integument. The obturator is in direct contact with the rim of the inner integument, but does not protrude into the micropyle. The semi-annular outer integument is four cell layers thick and the inner, lobed integument is six to eight cell layers thick. An endothelium is present. The nucellus disintegrates around the embryo sac. The floral base is concave and a short floral cup is present. Surrounding the gynoecium is a thin, dorsoventrally flattened cup-like nectary, which is nectariferous on its inner surface (Figs 65, 66). The nectary also extends onto the inner surface of the floral cup. The lateral walls of each carpel join the floral base above the dorsal side, resulting in deep nectariferous recesses. The pedicel is not clearly articulated.

**Anatomy:** Sepals have three main and one to three secondary vascular bundles and three vascular traces (including two smaller synlaterals). The median carpel bundle extends into the stigmatic branches, with the shorter lateral bundles extending into the base of the style. Additional lateral carpel bundles are present in the ovary wall. Above the placenta, lateral carpel bundles form synlaterals in the septa from which the ovules are supplied. The ovule bundle branches from the chalaza into the outer integument. Towards the base of the ovary neighbouring secondary lateral carpel bundles fuse, and those closest to the centre of the gynoecium, together with the dorsal carpel bundle, join the ring of bundles in the centre of the gynoecium. Small phloematic bundles extend into the base of the nectary rim, departing from the median sepal bundles in the floral cup. The lateral bundles in the outer part of the ovary wall join the large median sepal/nectary bundle complexes in the



**Figure 10.** *Drypetes madagascariensis* (Putranjivaceae). Floral bud, functionally male (morphologically bisexual), transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey. A–D, Free sepal parts (in D, inner sepals joining convex floral base); level of stamens (in B, C, dehisced anthers). A, Level of swollen attachment region of anthers. B–D, Level of nectary. B, C, Level of bicarpellate rudimentary gynoecium; level of nectary lobes with pointed tips. B, Level of free carpels. C, Level of united carpels. D–F, Floral base and pedicel. Scale bar, 500 µm.

floral cup. Sepal, gynoecial and nectary bundles join to form a central stele in the pedicel.

**Histology:** Uniseriate, c. four-cellular, lignified hairs are present along the sepal margins and on the dorsal sepal surface. Cells with oxalate druses are present in the sepals, gynoecium and nectary. Small amounts of tanniferous tissue are present in the sepals (mostly associated with the vascular bundles) and also in the gynoecium. Sclerenchyma is present in the ovary wall towards its periphery. Stomata are present on the dorsal sepal surface. Mucilage cells and special mucilage cells are absent.

#### *Drypetes madagascariensis (male)* Figures 10, 28, 44, 54, 62.

**Morphology:** Flowers are functionally male, but morphologically bisexual (Fig. 10). They are small and polysymmetric, with five sepals and (two–) three (–four) stamens; petals are absent. Two rudimentary carpels are present (Figs 10B, 44). Sepals form the protective organs still in advanced buds (Fig. 28), and remain upright and relatively closed in anthetic flowers with the stamens protruding between them. Sepals may be congenitally united for a short distance; in the free region, aestivation is quincuncial. Sepals have a broad base and a rounded apex, with fringed margins. The two outer sepals are conspicuously shorter and narrower than the inner ones (Fig. 28); they are not postgenitally connected. In flowers with three stamens, the stamens are on the radii of the three outermost sepals (Fig. 10C, D). Filaments are much longer than anthers at anthesis. Anthers are sagittate, dorsifixated towards the base of the anther, extrorse (to latrorse) and versatile (Figs 10A, B, 54, 62). Dehiscence is via longitudinal slits, which are not continuous over the anther apex. The endothecium is continuous over the ventral side

of the connective (and on the dorsal side only in the uppermost part of the connective); it is not continuous behind the thecae. Anthers have a broad connective and a short protrusion (Fig. 54). The attachment region of the anther to the filament is swollen on the dorsal side. The rudimentary gynoecium is syncarpous in its lower part, apocarpous above, with one carpel slightly longer than the other (Figs 10B, C, 44). Each carpel has a somewhat pointed apex. Carpels are solid. In the upper syncarpous zone, a central gap is present between the carpels. Three distinctive nectary lobes are present between the rudimentary gynoecium and the stamens, and alternate with the stamens (Figs 10B–D, 44). Each lobe has three parallel ridges, each ending in a pointed tip (Figs 10C, 44). Towards the convex floral base, the lobes fuse with each other and also partially with the rudimentary gynoecium and with the ventral side of the sepals (the filament bases are still free at this level) (Fig. 10D). The stamen filaments are the last organs to join the convex floral base.

**Anatomy:** Sepals have one to three main and one to three secondary vascular bundles and three vascular traces (the laterals forming synlaterals) (Fig. 10E). Stamens have a single vascular bundle. A single dorsal vascular bundle extends into the apex of each carpel of the rudimentary gynoecium; in the longer of the two carpels, two main lateral bundles are also present, extending into the lower part of the apocarpous zone (Fig. 10B). In the syncarpous zone, additional secondary lateral bundles are present (Fig. 10C). The nectary has numerous small phloematic bundles (Fig. 10D), which anastomose in the floral base, joining with the gynoecial bundles and also with the closest stamen bundles. Also in the floral base, bundles of adjacent sepals form synlaterals, and carpel bundles join into a single central bundle. Sepal traces are joined by neighbouring

stamen or nectary bundles to form bundle complexes (Fig. 10E). Together with the gynoecial bundles, they form a central stele in the pedicel.

**Histology:** Uniseriate, two- or three-cellular lignified hairs are present at the margins of the sepals (Fig. 28). Cells with oxalate druses are present in all floral organs and the nectary lobes. A small amount of tanniferous tissue is present in the sepals associated with the vascular bundles, in the rudimentary gynoecium and in the nectary. Stomata are scarce on the dorsal sepal surface. Sclerenchyma, mucilage cells and special mucilage cells are absent.

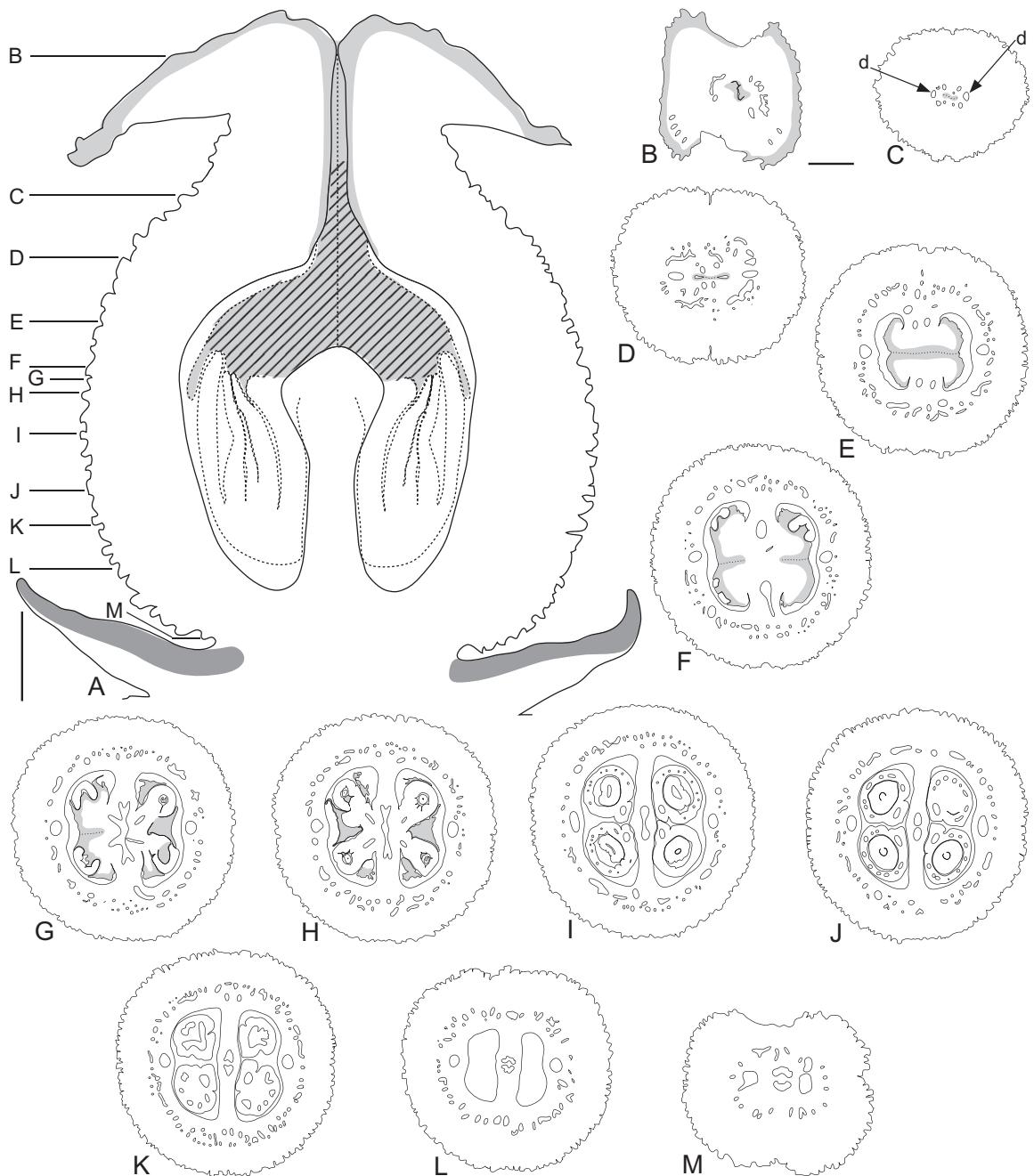
*Drypetes sp. (female)*

Figures 11, 42, 67, 74, 92, 93, 109D, 110.

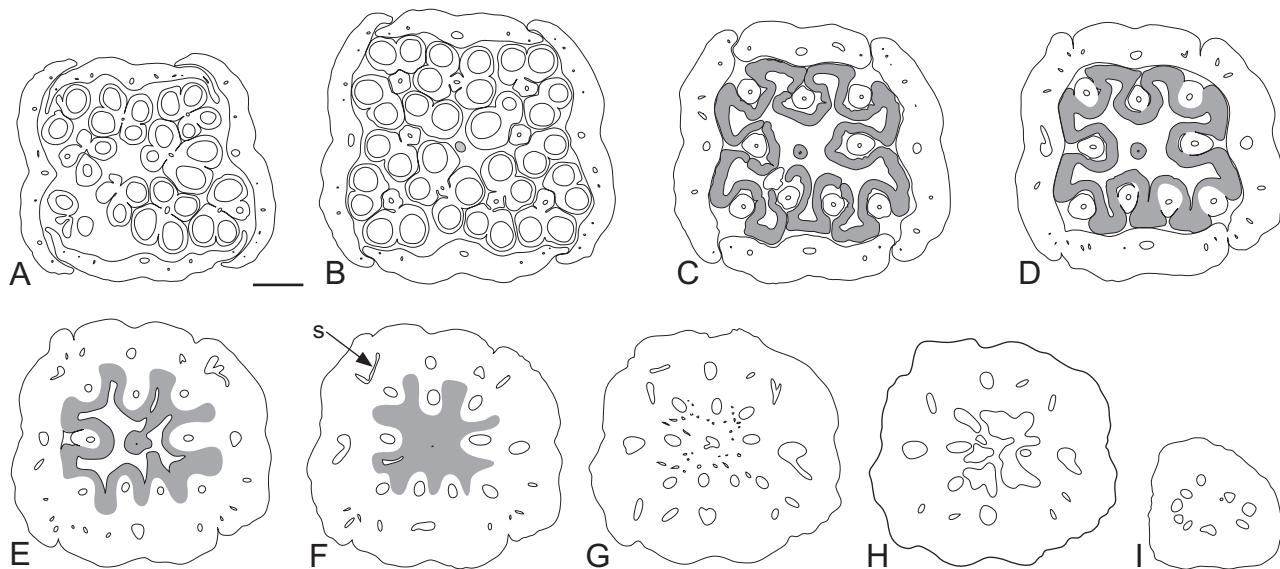
**Morphology:** The description is based on flowers after anthesis (sepals abscised), as buds were not available. The plants are ramiflorous with flowers emerging in clusters. Flowers are functionally and morphologically female; they are small and polysymmetric, with four sepals and two carpels; petals and stamens are absent. The gynoecium is syncarpous up to the lower part of the short style; it is of angiospermy type 4 (Fig. 11). Two large, almost sessile reflexed, shortly bilobed, dorsoventrally flattened stigmatic branches are present (Figs 11A, B, 67, 74); the receptive surface of the stigmas is nonpapillate; secretion is present. The superior ovary and style are covered by short, multiseriate, multicellular protuberances with shallow furrows between them (Fig. 11A, C–M); the stylar epidermis has two or three cellular papillae. A short gynophore is present. The ovary is synascidiate up to above the placenta (Fig. 11F). A ventral slit extends up to the base of the stigma; it is postgenitally fused in the upper symplicate zone of the style and in the ovary (Fig. 11C–E). It extends into the synascidiate zone as a postgenitally fused internal ventral furrow (Fig. 11F, G). PTTT lines the ventral slit in the upper symplicate zone of the style as c. seven cell layers, diminishing to three or four cell layers in the lower symplicate zone and to two or three cell layers in the symplicate zone of the ovary (Fig. 11A). PTTT also lines a short central gap in the style, which is secretion filled in its upper part (Fig. 11B). The ventral furrow is lined by two cell layers of PTTT, which appears to continue on the ventral wall of the locule for a short distance below the placenta. A compitum is present throughout the symplicate zone (Fig. 11A–E). Individual carpellary stylar canals are absent. Two large obturators span between the symplicate and synascidiate zones just above the placenta (Figs 11E–H, 92, 93). Placentation is axile. Two collateral, pendant antitropous ovules are present per carpel (Figs 11, 92); the upper face of

each ovule slopes downwards towards the neighbouring ovule within a locule (Fig. 11G). Ovules are bitegmic and anatropous; the nucellus is long and slender (Fig. 109D). The rim of the outer integument protrudes above that of the shorter inner integument, but does not take part in micropyle formation as its entrance is widely open; instead, the upwards facing micropyle is formed by the inner integument alone (Figs 11H, 109D). Both integuments are lobed, the outer integument especially on the raphal side; the two lobes of the outer integument form a shallow lateral slit (Fig. 11G), whereby lateral slits of the adjacent ovules within a carpel face each other. The rims of both integuments are in close contact with the obturator and the obturator protrudes downwards between gaps in the integuments, especially on the raphal side and through the lateral slit; it may also protrude into the micropyle (Figs 11F–H, 109D). The semi-annular, outer integument is seven cell layers thick, the inner seven to nine cell layers thick. An endothelium is present (Figs 109D, 110). The nucellus disintegrates around the embryo sac (Fig. 109D). At its base, the nucellus begins higher up on the raphal side than on the antiraphal side (Fig. 109D). The raphe forms a thickened ridge in which the vascular bundle is positioned. A continuous, thin, dorsoventrally flattened cup-shaped nectary surrounds the gynoecium (Figs 11A, 42, 67). The floral base is convex. The pedicel is not conspicuously articulated.

**Anatomy:** Sepals have one vascular trace. Main lateral carpel bundles extend into the stigmatic branches (Fig. 11B). The shorter dorsal carpel bundle extends into the upper symplicate zone of the style where, together with secondary and main lateral bundles, it forms a dorsal band of bundles, which separates into individual bundles lower down in the style (Fig. 11C). Additional secondary carpel bundles extend into the ovary wall and anastomose (Fig. 11E–L). Lateral carpel bundles form synlaterals in the ovary septum (Fig. 11E, F); these synlaterals supply the ovules (Fig. 11G–I). The ovular bundle branches from the chalaza into the outer integument (Figs 11I–K, 109D). Additional large lateral bundles are present in the ovary wall close to the septum. Below the placenta, the septal synlaterals join to form a bundle complex in the centre of the gynoecium. Above the gynophore, secondary lateral bundles join the dorsal bundle or neighbouring lateral bundles, and these enlarged bundles join the ring of bundles in the centre of the gynophore (Fig. 11M). Phloematic bundles extend into the base of the nectary and join with the gynoecial bundles in the floral base. The resulting complex bundles, together with the sepal bundles, form a central stele in the pedicel.



**Figure 11.** *Drypetes* sp. (Putranjivaceae). Bicarpellate gynoecium from female flower after anthesis; pollen tube transmitting tract (PTTT) shaded light grey. A, Schematic median longitudinal section. Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines; d, dorsal carpel vascular bundle; postgenitally fused areas are hatched; nectary shaded dark grey. B–M, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines. B–E, Level of symplicate zone and compitum. B, Level of stigma and secretion-filled gap in centre of gynoecium. C–E, Level of postgenitally fused ventral slits. D, Level of short stylar canals. F–K, Level of collateral ovules with lobed integuments. F–H, Level of obturators protruding between integuments. F, G, Level of postgenitally fused internal ventral furrows. G, H, Level of placenta; level of upper face of ovules sloping downwards towards neighbouring ovule (lateral slits in outer integument). I–K, Level of ovules with numerous vascular bundles in outer integument. J, Level of nucellus beginning higher up on the raphal than the antiraphal side. K, Level of ovule vasculature branching from chalaza. L, Below level of ovules. M, Gynophore. Scale bars, 500 µm.



**Figure 12.** *Drypetes* sp. (Putranjivaceae). Floral bud, functionally male (morphologically bisexual), transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey; s, sepal synlateral. A–D, Level of stamens. A–C, Free sepal parts. B–D, Level of nectariferous rudimentary gynoecium. C–F, Level of nectary; in C, D, nectary sinuously curved around the inside of the stamen filaments. D, E, Level of stamen bases. D, Level of united sepals. E–G, Level of sepal bundles forming synlaterals. E, Level of floral cup with nectary lining inner surface. F–I, Floral base and pedicel. Scale bar, 500 µm.

**Histology:** Uniseriate, three- or four-cellular, lignified hairs are present, densely covering the pedicel, ovary and the dorsal side of the stigmatic branches; similar hairs are sparse on the pedicel. Tanniferous tissue is present in the gynoecium and nectary. Cells with oxalate druses are present in the gynoecium (including ovules) and nectary. Below the placenta, the tissue of the ovary septum is slightly spongy, with loosely arranged small cells. Sclerenchyma, mucilage cells and special mucilage cells are absent.

#### *Drypetes* sp. (male)

Figures 12, 43.

**Morphology:** The description is based on floral buds, as no anthetic flowers were available. The plants are ramiflorous with clusters of flowers at different developmental stages. Flowers are functionally male, but morphologically bisexual (Fig. 12). They are small and polysymmetric, with four sepals, eight to ten stamens and one rudimentary solid carpel (Fig. 12C–E). Petals are absent. The relatively thick sepals form the protective organs still in advanced buds. They are congenitally united at their base (Fig. 12D) with a decussate arrangement in their free parts; they are not postgenitally connected. They have a broad base and a pointed tip. The inner stamens are anterosepalous and the outer ones alternisepalous (Fig. 12C, D).

When more than eight stamens are present, the additional stamens are in double position opposite the sepals (Fig. 12C, D). Anthers are elongate 'X'-shaped, basifix, extrorse (outer stamens) to latrorse (inner stamens) and nonversatile. The connective is narrow and relatively thick; a protrusion is absent. Thecae dehisce via longitudinal slits, which are not continuous over the anther apex. The endothecium is not continuous over the connective or behind the thecae. A dorsoventrally flattened, cup-shaped nectary is present between the stamens and rudimentary carpel (the base of which also appears secretory) (Fig. 12E). Its rim curves sinuously around the stamen filaments and is continuous with the base of the filaments (Figs 12C, 43). It fuses with the alternisepalous stamens above the anterosepalous ones (Fig. 12D). The floral base is concave; the stamen filaments join with sepals to form a floral cup whose inner surface is nectariferous (Fig. 12E). The pedicel is not conspicuously articulated.

**Anatomy:** Sepals have three main and four to six secondary vascular bundles and mostly three vascular traces (including synlaterals). Stamens have a single vascular bundle. A single bundle extends into the base of the rudimentary carpel (Fig. 12C–E). At the floral base, lateral sepal bundles fuse and others form synlaterals with bundles of adjacent sepals

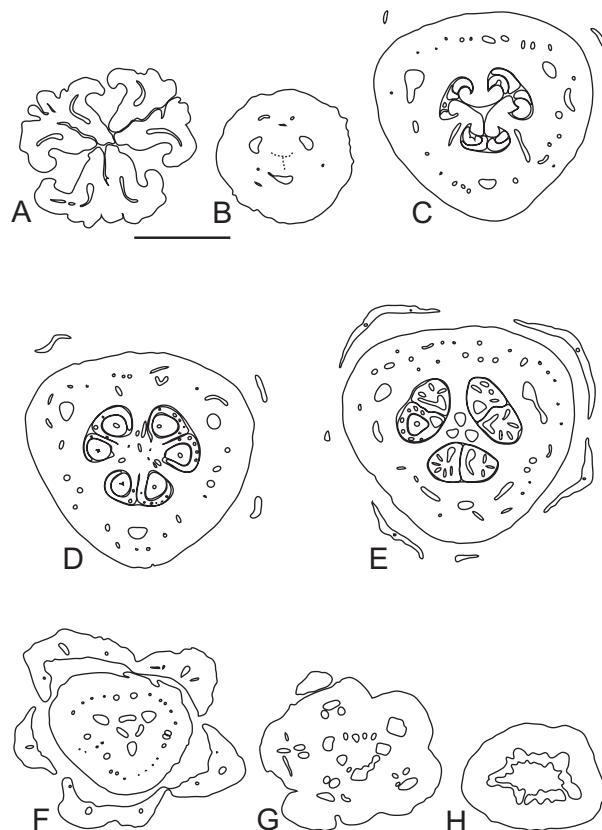
(Fig. 12E, F). Smaller bundles, which may supply the nectary, extend into the centre of the floral base (Fig. 12G). The outer of these smaller bundles joins the closest stamen bundles, the remainder fusing with neighbouring bundles in the centre of the flower. These bundle complexes join the sepal traces in the pedicel to form a central stele.

**Histology:** Uniseriate, three-cellular, lignified (tanniferous) hairs are present on the dorsal surface of the sepals and along their margins; mostly unicellular hairs are dense on the ventral side of the sepals. In addition, long, narrow, unicellular, unlignified hairs are present on the nectary (Fig. 43). Tanniferous tissue, mostly associated with the vasculature, is present in the sepals. Stomata are present on the dorsal surface of the sepals. Cells with oxalate druses are present in the sepals and anthers. The tissue of the stamen filaments appears spongy with large intercellular spaces. Sclerenchyma, mucilage cells and special mucilage cells are absent.

*Putranjiva roxburghii (female)*

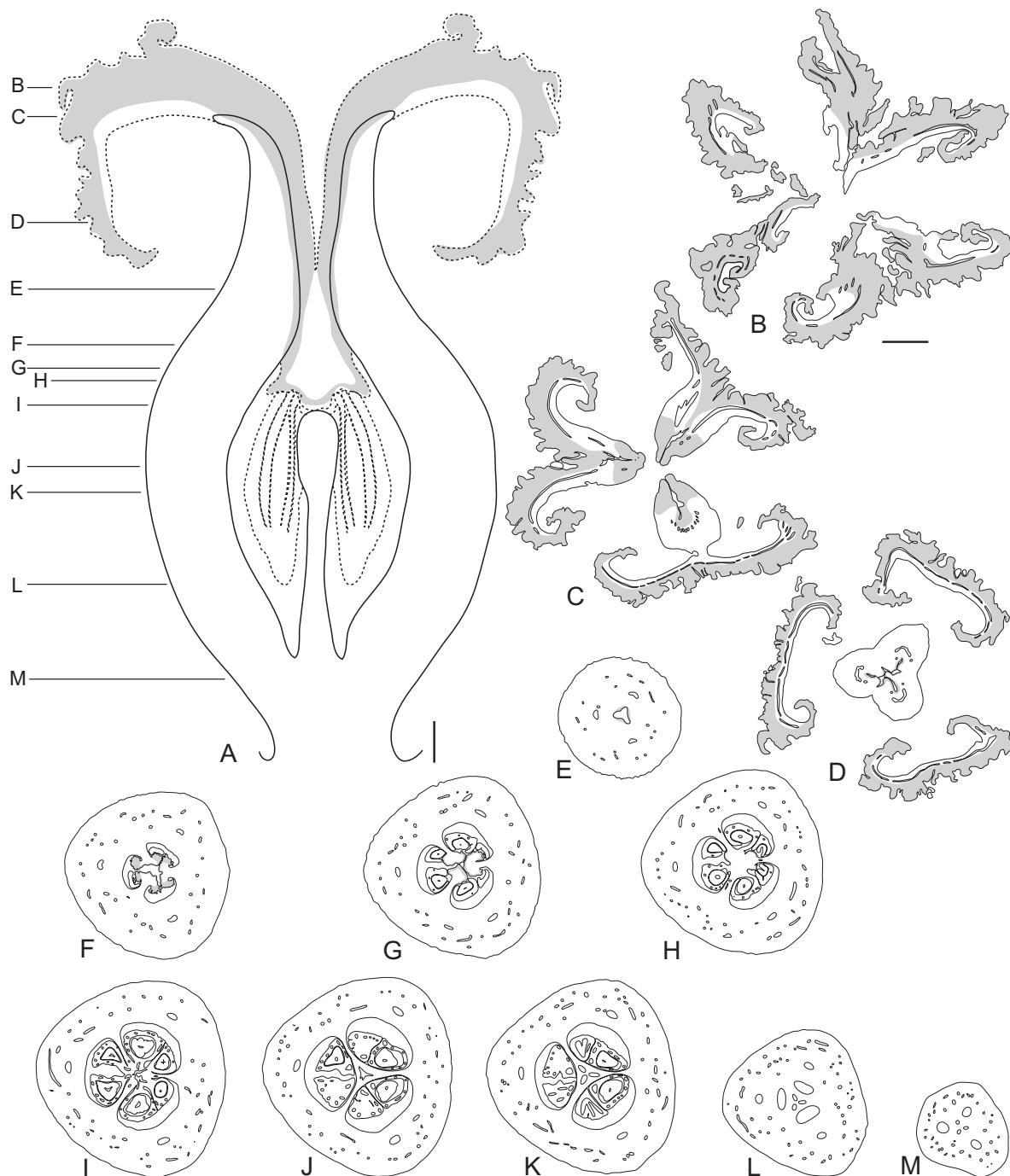
Figures 13, 14, 21, 22, 36, 64, 73, 85, 86, 97–100, 109E.

**Morphology:** Plants are dioecious. Flowers are functionally and also morphologically female. They are small and polysymmetric, with five sepals and three carpels (Figs 13, 14, 22). Petals and stamens are absent. Sepals are short and appear to only form the protective organs in the earliest developmental stages, as the gynoecium is already longer than the sepals in young buds (Figs 21, 22, 64); they abscise after anthesis. Sepals are shortly congenitally united (Fig. 13F); aestivation is open in the free parts (Fig. 13C–F). The two outer sepals are shorter and narrower than the inner three. Sepals have a pointed apex and fringed margins (Fig. 36). The gynoecium is syncarpous up to the base of the stigmatic branches (Fig. 14A, D–L); it is of angiospermy type 2. The superior ovary has a short style and is elevated on a gynophore (Fig. 14A, M). It is synascidiate up to above the placenta (Fig. 14A, H–L). The already reflexed stigmatic branches enlarge massively during development and, at anthesis, the margins of each lobe reflex further, rolling outwards to further expose the receptive surface from above and from the side – this rolling back of the lobes results in a stigma with two crescent-shaped horns (Figs 14A–D, 64, 73). The stigmatic surface is covered by multicellular protuberances (Figs 14A–D, 73); stigmatic secretion appears to be present at anthesis. An open ventral slit extends up to the base of the stigmatic branches (Figs 14A, C, 73); in the upper part of the style, it is closed at its flanks, open along its inner angle and a



**Figure 13.** *Putranjiva roxburghii* (Putranjivaceae). Floral bud, morphologically female, transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines. A, Level of free carpels (plicate zone) and stigmatic branches. B, C, level of symplicate zone of gynoecium. B, Level of style and postgenitally fused ventral slits. C–F, Free sepal parts (in F, some sepals united) with open aestivation. C–E, Level of collateral ovules. D, E, Level of synascidiate zone. D, Level of placenta. F, Level of gynophore. G, H, Floral base and pedicel. Scale bar, 500 µm.

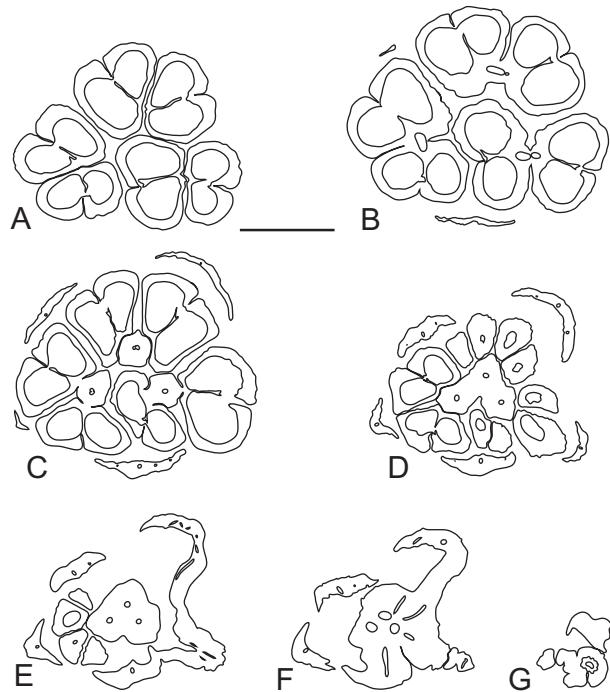
stylar canal is present within each carpel; the slit may be postgenitally fused (or simply closed in some carpels) in the lower part of the style (Figs 13B, 14C, D) and is open directly above the ovary locules and within the symplicate region of the ovary (Fig. 14E, F); the ovary is unilocular in this region. PTETT is present as c. ten cell layers on the receptive surface of the stigmatic branches and also lining the open ventral slits in this region (Fig. 14A). In the upper style, c. four cell layers line the styalar canals, diminishing to two cell layers lower down in the style. The incomplete ovary septa are lined by one or two layers of PTETT; the epidermis is papillate. A compitum appears to be present throughout the symplicate zone



**Figure 14.** *Putranjiva roxburghii* (Putranjivaceae). Tricarpellate gynoecium from female flower at anthesis; pollen tube transmitting tract (PTTT) shaded grey. A, Schematic median longitudinal section with two carpels projected in the median plane. Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines. B–M, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines. B–D, Level of reflexed stigmatic branches. B, C, Level of free carpels (plicate zone). C–G, Level of open ventral slits. D–G, Level of symplicate zone and compitum. D, E, Level of style with central gap. F–K, Level of collateral ovules. F, G, Level of unilocular ovary; level of obturators. G–K, Level of ovules with numerous vascular bundles in outer integument. H–K, Level of synascidiate zone. H, Level of ovules with a lateral slit in rim of the outer integument (upper face of ovules sloping away from the adjacent ovule). K, Level of ovular bundles branching from chalaza. L, Below the level of the ovules. M, Gynophore. Scale bars: 200 µm (A), 500 µm (B–M).

(Fig. 14C–G). An apical septum is absent. Two obturators are present in each carpel, predominantly in the symplicate region and continuing for a short distance into the synascidiate zone just above the placenta (Figs 14F, G, 85, 86). The placenta is axile. Two collateral pendant, antitropous ovules are present per carpel (Fig. 85). The upper face of each ovule slopes downwards towards either the ventral or lateral side of the carpel (Figs 13D, 14H). Ovules are bitegmic, anatropous and probably incompletely tenuinucellar; the nucellus is conspicuously long and slender (Fig. 109Ei, Eii). The rim of the outer integument mostly protrudes above that of the inner integument, but does not take part in micropyle formation as its entrance is widely open; instead the long, upwards facing transverse slit-like micropyle is formed by the inner integument alone (Figs 97–100, 109Ei, Eii). There is a space between the integuments; it is especially conspicuous in the lower part of the ovules (Figs 97, 98, 100, 109Ei, Eii). Obturators protrude between the gaps in the integuments and come into direct contact with the entrance of the micropyle, but do not protrude into it (Fig. 109Ei, Eii). Both integuments are lobed (Fig. 100); the two lobes of the outer integument may form a shallow lateral slit, whereby lateral slits of the adjacent ovules within a carpel face away from each other (Figs 14H, 100). The semi-annular outer integument is four or five cell layers thick, the inner integument five to eight cell layers. An endothelium is present (Fig. 109Ei, Eii). The nucellus appears to disintegrate around the embryo sac. The raphe forms a ridge in which the vascular bundle is positioned. The floral base is convex. A nectary is absent (flowers appear to be wind pollinated). The pedicel is articulated at its base.

**Anatomy:** Sepals have one to three main and one or two secondary vascular bundles and a single vascular trace (Fig. 13G). Branches of the dorsal carpel bundle (or longer lateral bundles?) extend into the stigmatic lobes (Fig. 13A); lower down at the base of the stigmatic branches, they form a dorsally positioned crescent-shaped band of bundles (Fig. 14C), which extends downwards into the style. Additional lateral bundles extend into the lower style and anastomose with the dorsal bundle in the ovary wall (Fig. 13E); carpel synlaterals are present in the lower style and ovary septa. Additional lateral bundles extend into the placenta and supply the ovules (Fig. 14I). The ovule bundle branches massively from the chalaza into the outer integument (Figs 13D, E, 14G–K, 109Ei, Eii). In the centre of the gynophore, the dorsal and main synlateral bundles (from the septa) form a triangular ring of bundles (Fig. 13F, G). Lateral sepal bundles join the median bundle at the base of the sepals. In the floral base, the sepal traces are joined



**Figure 15.** *Putranjiva roxburghii* (Putranjivaceae). Floral bud, morphologically male, transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines. A–E, Level of stamens. B–F, Free sepal parts with open aestivation (in E, three sepals united). D, E, Level of united stamen filaments. F, G, Floral base and pedicel. Scale bar, 500 µm.

by the closest secondary lateral carpel bundles to form five bundle complexes. In the pedicel, the sepal–carpel complexes and central gynoecial bundles unite into a central stele.

**Histology:** Uniseriate, three- to five-cellular, lignified hairs are present on the pedicel, the dorsal side and margin of the sepals and on the gynoecium, including the dorsal side of the stigma, and are dense on the style and ovary (Fig. 22). Tanniferous tissue appears to be mostly absent, except in the mature stigma and also in the upper part of the sepals. Cells with oxalate druses are present in the sepals and gynoecium. Slightly raised stomata are present on the dorsal side of the sepals, especially towards their base. Patches of sclerenchyma are present in the ovary wall. Mucilage and special mucilage cells are absent.

*Putranjiva roxburghii (male)*  
Figures 15, 23, 50, 58.

**Morphology:** The plants appear to be ramiflorous with the flowers in clusters of different developmental stages. Flowers are functionally and morphologically male and are small and polysymmetric (Figs 15, 23). They have five sepals and (two–) three (–four) stamens. Petals and carpels are absent. Sepals form the protective organs only in very young buds; in advanced buds, they are no longer protective (Figs 15, 23). Sepals are shortly congenitally united (Fig. 15E) and have an open aestivation in their free parts (Fig. 15B–F). They are narrow and have fringed margins. Stamen maturation and dehiscence appear to be staggered within a flower. Filaments are shorter or equally long as anthers at anthesis; they are united at their base (Fig. 15E). When three stamens are present, they appear to be in the radii of the outer three sepals (Fig. 15D). Anthers are 'X'-shaped, extrorse, dorsifixated towards the base and nonversatile (Figs 50, 58). The connective is narrow and thin; a protrusion is absent. Anther dehiscence is via longitudinal slits, which are not continuous over the anther apex. The endothecium is not continuous over the connective or behind the thecae. In dehisced anthers, the remains of the thecal septum are relatively massive. The floral base is convex. A nectary appears to be absent (apparently wind pollinated). The short pedicel is not obviously articulated.

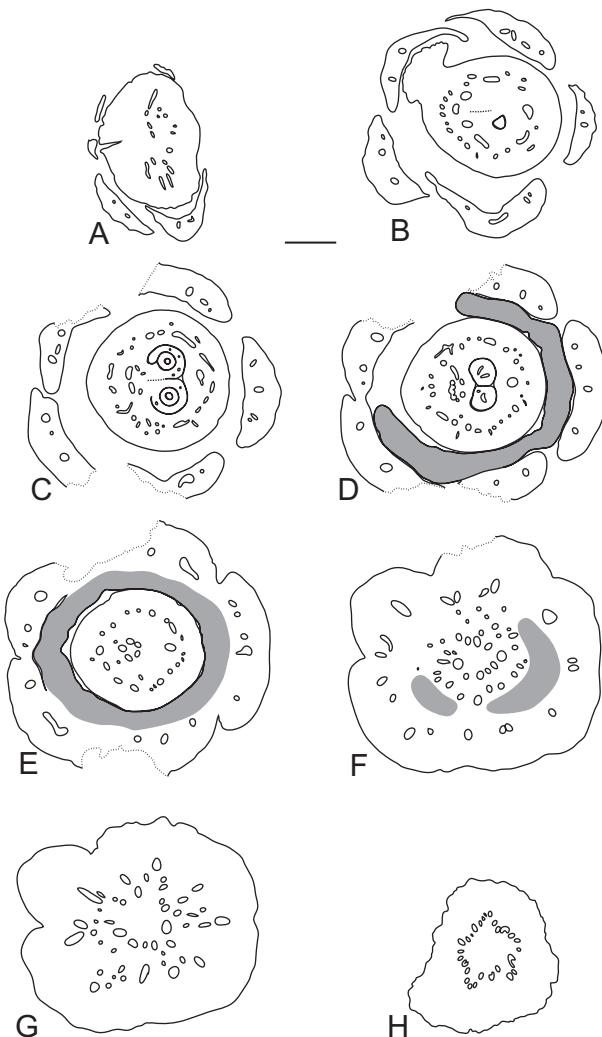
**Anatomy:** Sepals have one to three main and sometimes one secondary vascular bundle and one to three vascular traces (Fig. 15E, F). Stamens have a single broad vascular bundle. In the floral base, sepal traces are joined by the closest stamen bundles to form a central stele in the pedicel (Fig. 15F, G).

**Histology:** Unicellular hairs are present on the dorsal surface and along the margins of the sepals, on both sides of the anthers (Figs 23, 50, 58) and on the pedicel; those on the anthers are unlignified. Tanniferous tissue is scarce in the sepals. Cells with oxalate crystals are present in the sepals and anthers. Stomata are present on the dorsal side of the sepals. Sclerenchyma, mucilage cells and special mucilage cells are absent.

#### Sibangea arborescens (*female*)

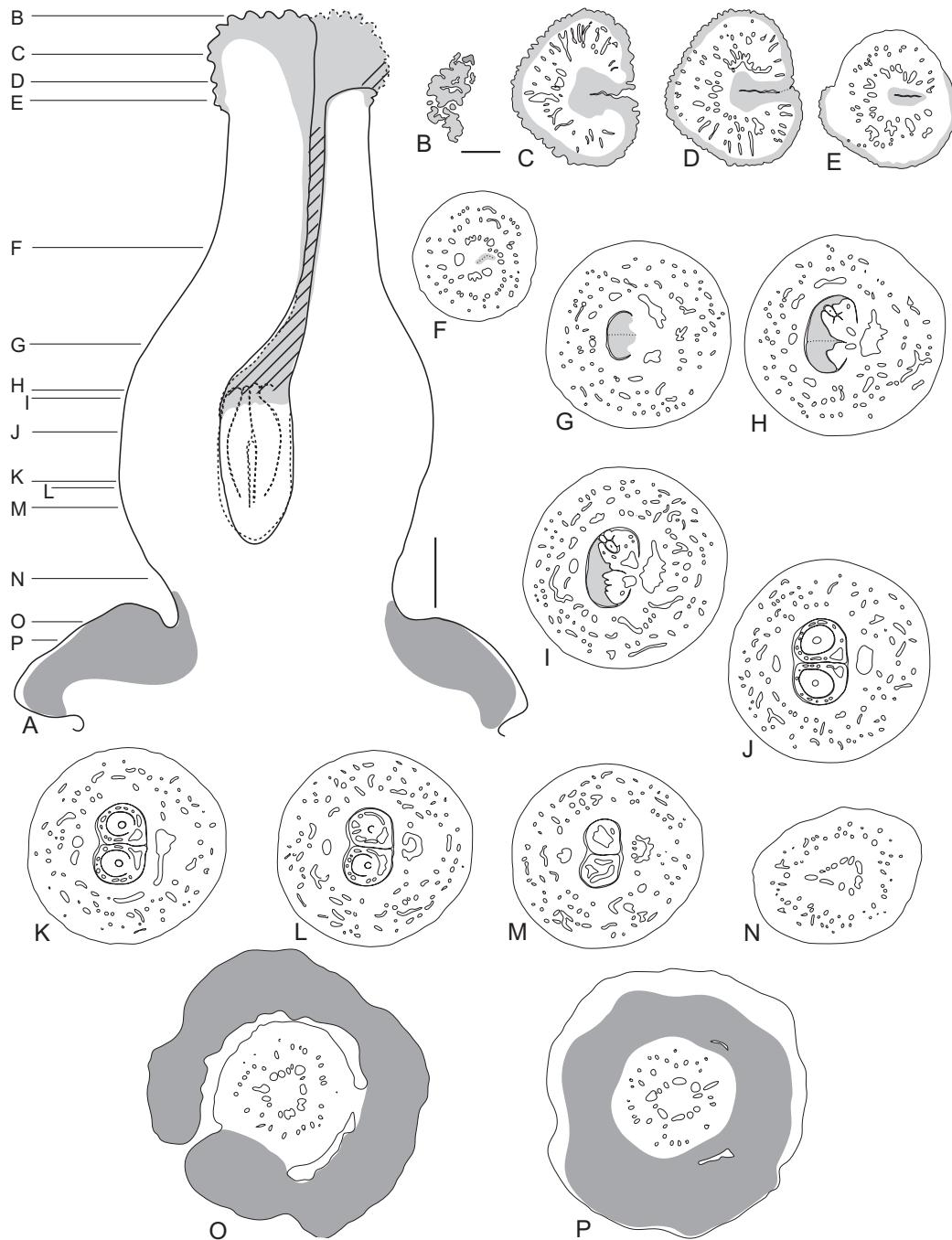
Figures 16, 17, 40, 70, 81, 82, 87, 88, 101, 102, 109F, 111

**Morphology:** Flowers are functionally and morphologically female. They are small and polysymmetric, with five (–seven) sepals and a single fertile carpel (Figs 16, 17). Petals and stamens are absent. The sepals are short and are only protective in the early bud stages, the gynoecium already protruding from the sepals in advanced floral buds. Sepals may be



**Figure 16.** *Sibangea arborescens* (Putranjivaceae). Floral bud, morphologically female, transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines; nectary shaded grey; in C–E, herbivore damage of sepals indicated by dotted lines. A–D, Free sepal parts with open aestivation (in D, two sepals united). A, Level of stigma and style. B–D, Level of collateral ovules. B, C, Level of postgenitally fused internal ventral furrow in ovary. C, Level of placenta. D–F, Level of nectary. E, Level of floral cup and gynophore. F–H, Floral base and pedicel. F, G, Level of sepal bundles forming synlaterals. Scale bar, 500 µm.

shortly congenitally united (Fig. 16E); aestivation is quincuncial in the free parts in young buds with five sepals; in older buds, aestivation is mostly open; sepals are not postgenitally connected in bud. Sepals have a more or less pointed tip. The outer two sepals are narrower than the inner three. Secretory colleter-



**Figure 17.** *Sibangea arborescens* (Putranjivaceae). Monocarpellate (pseudomonomerous?) gynoecium from female flower at anthesis; pollen tube transmitting tract (PTTT) shaded light grey. A, Schematic median longitudinal section (dorsal side left). Morphological surface drawn with a continuous line; outline of parts just out of the median plane drawn with broken lines; postgenitally fused areas are hatched; nectary shaded dark grey. B–P, Transverse section series; morphological surface indicated by thicker continuous lines; vasculature by thinner continuous lines; postgenitally fused areas indicated by broken lines; nectary shaded dark grey. B–E, Level of stigma. B–D, Level of plicate zone. C, Level of open ventral slit. F–H, Level of postgenitally fused internal ventral furrow. G–I, Level of obturators. H–M, Level of collateral ovules. H, I, Level of placenta with obturator protruding downwards into locule; level of upper face of ovules sloping downwards away from attachment of ovule. K, Level of inner integument beginning higher up on the raphal than the antiraphal side. L, Level of nucellus beginning higher up on the raphal than the antiraphal side. M, Level of ovular bundles branching from chalaza. N, Gynophore. O, P, Level of nectary. Scale bars, 500 µm.

like structures are present along the sepal margins. In bud, the floral apex is concave and a floral cup is present (Fig. 16E). At anthesis, the floral apex becomes convex and a prominent nectary disc surrounds the gynoecium (Fig. 17O, P), which, in bud, lines the floral cup (Fig. 16E). The gynoecium is of angiospermy type 2. It is ascidiate up to the lower part of the stigma (Fig. 17E–M). The gynoecium has a capitate stigma, a short thick style and a superior, rounded ovary (Figs 17A, 70, 81, 82) elevated on a gynophore (Figs 16E, 17N, O). The ovary base has one or two bumps on the ventral side of the fertile carpel; if the gynoecium is pseudomonomerous, these bumps may represent the rudiments of one or two reduced carpels (Fig. 70). The stigma is nonpapillate; its receptive surface has a network of short ridges (Fig. 17A, B); secretion appears to be present at anthesis. An open ventral slit is only present in the stigma (Figs 17C, 81). At the transition from plicate to ascidiate, the ventral slit is postgenitally fused (inner parts open) (Fig. 17D) and a short stylar canal extends into the upper ascidiate zone. Below this, the slit extends into the ascidiate zone as a postgenitally fused ventral furrow (Fig. 17F, G). In the stigma, PTTT lines the ventral slit and the receptive surface as 13–15 cell layers, diminishing to five to seven cell layers in the lower ascidiate zone of the stigma where it lines the stylar canal. In the style, PTTT is present lining the postgenitally fused ventral furrow as four cell layers. In bud, the locule bulges conspicuously upwards on the dorsal side (Fig. 16B). Large nonpapillate obturators are present, which completely surround the upper part of the ovules (Figs 17G–I, 87, 88, 109F). Placentation is apical and axile. Two collateral, pendant antitropous ovules are present per carpel (Figs 16C, 17H–M, 87, 88). The upper face of the ovules may slope downwards towards the dorsal side (Figs 17H, I, 101). Ovules are bitegmic, anatropous and incompletely tenuinucellar; the nucellus is conspicuously long and slender (Fig. 109F). The upwards directed micropyle is formed by the longer inner integument (Figs 102, 109F). Both integuments are lobed (Figs 17H, I, 102), with conspicuous slits in the rim of the outer integument; these slits may vary in position: in bud, they are positioned laterally (slits of adjacent ovules within a locule facing away from each other) (Fig. 16C), or medianly in anthetic flowers. Each obturator is in direct contact with the rims of the integuments and protrudes between the integuments (Figs 17H, I, 109F); it does not protrude into the micropyle. The semi-annular outer integument is five cell layers thick, the inner integument seven or eight cell layers. An endothelium is present (Figs 109F, 111). The nucellus disintegrates around the embryo sac (Fig. 109F). At their base, the inner integument and nucellus begin higher up

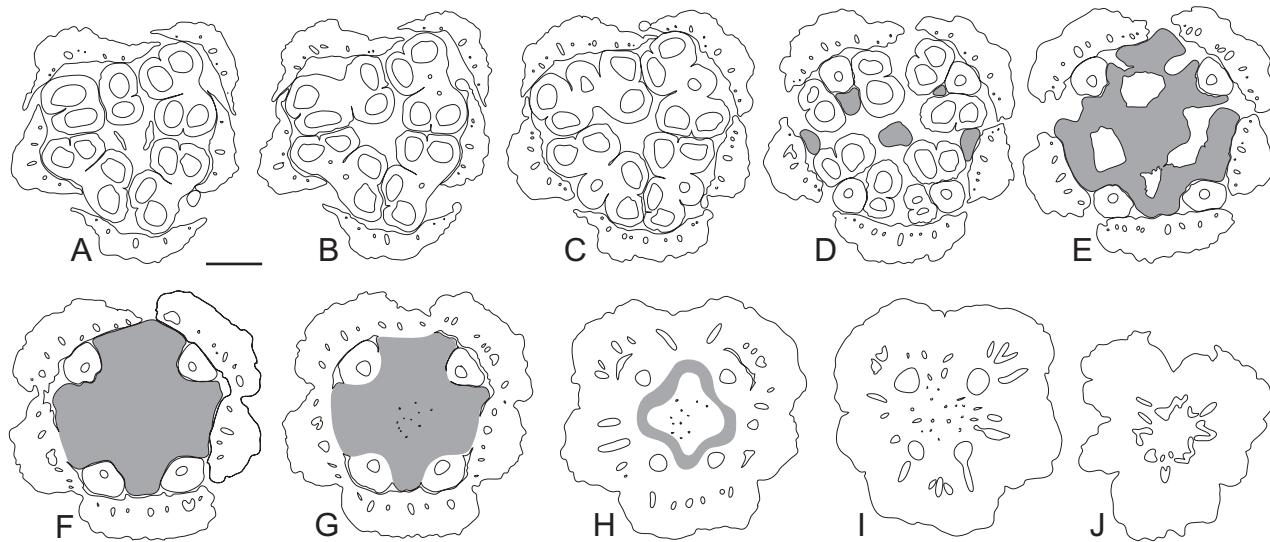
on the raphal side than on the antiraphal side (Fig. 109F). The pedicel appears to be articulated at its base.

**Anatomy:** Sepals have three main and one or two secondary lateral vascular bundles and three vascular traces (which may include synlaterals) (Fig. 16F, G). A dorsal carpel bundle plus numerous lateral bundles extend into the base of the stigma, surrounding the ventral slit as an inner and outer series of bundles (Fig. 17E); the main lateral bundles are included in the inner series. At the level of the upper part of the locule, neighbouring lateral bundles unite to form a large ventral bundle; branches from this bundle supply the ovules (Fig. 17H, I). The ovule bundle branches from the chalaza, raphe and placenta into the outer integument (Figs 16C, D, 17H–M, 109F). In the gynophore, the large ventral bundle (which supplies the ovules) expands into a ring of bundles (Fig. 17N, O). This ring of bundles is joined by the smaller lateral bundles and also the dorsal carpel bundle from the fertile carpel; an outer ring of lateral bundles remains separate from the others and only joins the central ring of bundles in the floral base (Fig. 17P). The base of the nectary is supplied by numerous small phloematic bundles. These bundles depart from the gynoecial bundles in the floral base. Sepal traces and gynoecial/nectary complexes join in the pedicel to form a central stele.

**Histology:** Uniseriate, two- or three-cellular lignified, tanniferous hairs are present on the dorsal surface of the sepals and especially along the margins and on the pedicel. Tanniferous tissue is scarce in the sepals (more abundant in sepals from buds), gynoecium (most abundant in the stigma) and in the nectary. Cells with oxalate druses are present in the sepals, gynoecium and nectary. Stomata are present on the dorsal side of the sepals, scarce on the style and gynophore, and are present on the nectary. The outer epidermis of the inner integument is distinct from the other cell layers as it is composed of small, square cells. Sclerenchyma, mucilage cells and special mucilage cells are absent.

*Sibangea arborescens* (*male*)  
Figures 18, 26, 33–35, 47, 49, 57.

**Morphology:** Flowers are functionally male, but morphologically bisexual. They are small and polysymmetric with five sepals and three or four stamens (Fig. 18). Petals are absent. A potential rudimentary gynoecium is present as a short nectariferous protuberance in the centre of the flower (Fig. 18D). Sepals form the protective organs in advanced buds (Fig. 26). They are congenitally united at the base (Fig. 18F, G)



**Figure 18.** *Sibangea arborescens* (Putranjivaceae). Floral bud, functionally male (morphologically bisexual), transverse section series; morphological surface indicated by thicker continuous lines; vasculature and histological (secondary) inner surface (pollen sacs) indicated by thinner continuous lines; nectary shaded grey. A–F, Level of stamens. A–E, Free sepal parts. A, B, Level of sepals with quincuncial aestivation. B, Level of anthers with two collateral vascular bundles in connective. D–H, Level of nectary. D–F, Level of sepals with open aestivation (in F, sepals partly united). D, Level of nectariferous solid rudimentary gynoecium. F–J, Level of convex floral base and pedicel. G, Level of stamens joining floral base. I, Level of joining stamen and sepal bundles. Scale bar, 500 µm.

with quincuncial aestivation in their upper parts in bud (Fig. 18A–C), but open aestivation lower down (Fig. 18D, E); they are not postgenitally connected in bud. Sepals are narrow and strap-like and of similar size (Figs 33, 34). They have a rounded apex, with secretory colleters-like structures along the margins (Figs 33–35). Stamens appear to be on the radii of the outer three sepals, with a double position in the radius of sepal 2 (Fig. 18E–G). Their filaments are longer than anthers already in bud, much longer at anthesis. Anthers are 'X'-shaped, dorsifixed towards the base, introrse (to latrorse) and nonversatile (Figs 49, 57). The connective is broad and relatively thin; a protrusion is absent. The filament is thickened at the attachment region of the anther (Fig. 49). Thecae dehisce by longitudinal slits, which are not continuous over the anther apex. An endothecium was not apparent at the bud stage studied; however, the cells of the hypodermis of the pollen sacs are larger than the other thecal cells; these large cells are not continuous across the connective or behind the thecae. The convex floral centre is nectariferous and extends as a dorsoventrally flattened and undulating disc whose rim covers the bases of the stamen filaments. The pedicel is not conspicuously articulated.

**Anatomy:** Sepals have three main and six or seven secondary vascular bundles and three or four vascu-

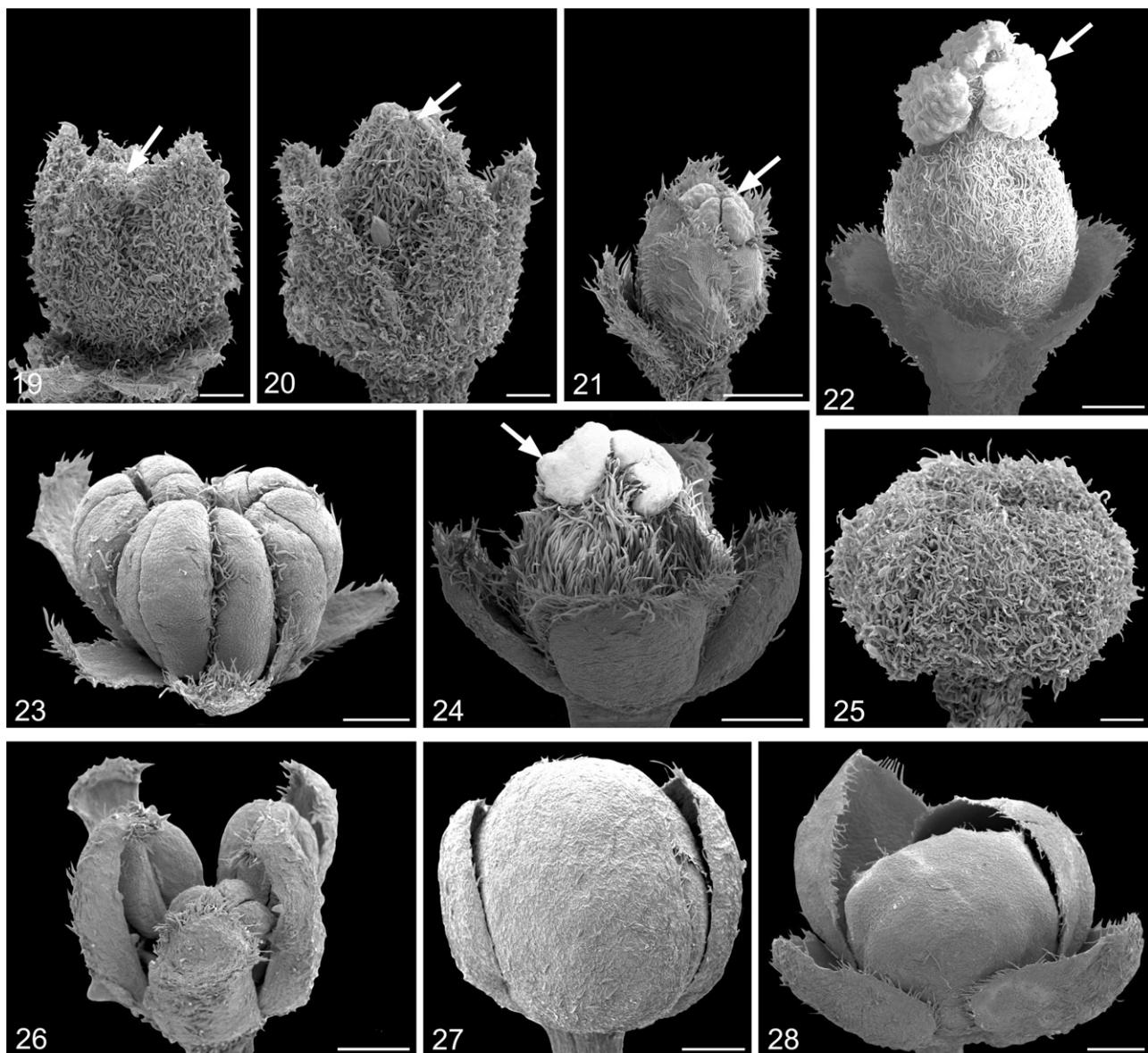
lar traces (Fig. 18H, I). Stamens have a single vascular bundle which may branch into two bundles in the upper part of the anther (Fig. 18B). Small phloematic bundles extend into the floral base and supply the nectary (Fig. 18G). These bundles fuse with the closest stamen bundle (Fig. 18I). Also at this level the stamen bundles fuse with the closest sepal trace, either median or lateral traces, depending on whether the stamens are in single or double position. All bundles together form a central stele in the pedicel.

**Histology:** Uniseriate, two-cellular, lignified tanniferous hairs are present on the dorsal sepal surface and on the pedicel. Stomata are present on the dorsal surface of the sepals. Tanniferous tissue is present in the sepals (scarce), stamens and nectary. Cells with oxalate druses are present in the sepals and anthers. Sclerenchyma, mucilage cells and special mucilage cells are absent.

## DISCUSSION

### DEVELOPMENT OF MACROSYSTEMATICS IN THE CLADE OF LOPHOPYXIDACEAE AND PUTRANJIVACEAE

As mentioned in the Introduction, a sister relationship between Lophopyxidaceae and Putranjivaceae was first found by Wurdack *et al.* (2004) and, since then, confirmed with progressively better support

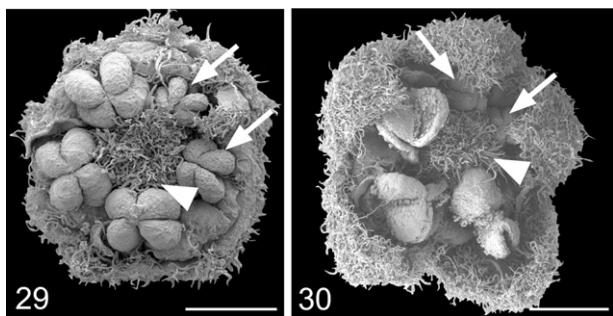


**Figures 19–28.** Entire floral buds; antesepalous view (in Figs 19 and 20: alternisepalous/antepetalous). Figures 19–24. Sepals not protective in older buds (arrow, gynoecium). Figures 19 and 20. *Lophopyxis maingayi* (Lophopyxidaceae); female. Figure 19. Very young bud with gynoecium slightly shorter than open sepals. Figure 20. Slightly older bud; gynoecium emerging above level of open sepals. Figures 21–23. *Putranjiva roxburghii* (Putranjivaceae). Figures 21 and 22. Female. Figure 21. Very young bud; gynoecium emerging above level of sepals. Figure 22. Advanced bud; sepals surrounding base of gynoecium. Figure 23. Male; advanced bud; sepals surrounding base of stamens. Figure 24. *Drypetes lateriflora* (Putranjivaceae); female; advanced bud, sepals surrounding base of gynoecium. Figures 25–28. Sepals protective in older buds. Figure 25. *Lophopyxis maingayi* (Lophopyxidaceae); male. Figure 26. *Sibangea arborescens* (Putranjivaceae); male; sepals opening (artefact); stamens shorter than level of sepals. Figures 27 and 28. *Drypetes madagascariensis* (Putranjivaceae); outer sepals shorter than inner sepals. Figure 27. Female. Figure 28. Male. Scale bars, 200 µm (Figs 19, 20, 25); 500 µm (Figs 21–24, 26–28).

(Davis *et al.*, 2005; Wurdack & Davis, 2009; Xi *et al.*, 2012). In the following two sections, a short outline of the convoluted systematic history of each of the two families is presented.

#### *Lophopyxidaceae*

When *Lophopyxis* Hook.f. was first described, Hooker (1887) tentatively (with a question mark) placed it in Euphorbiaceae. In his treatment of Euphorbiaceae,

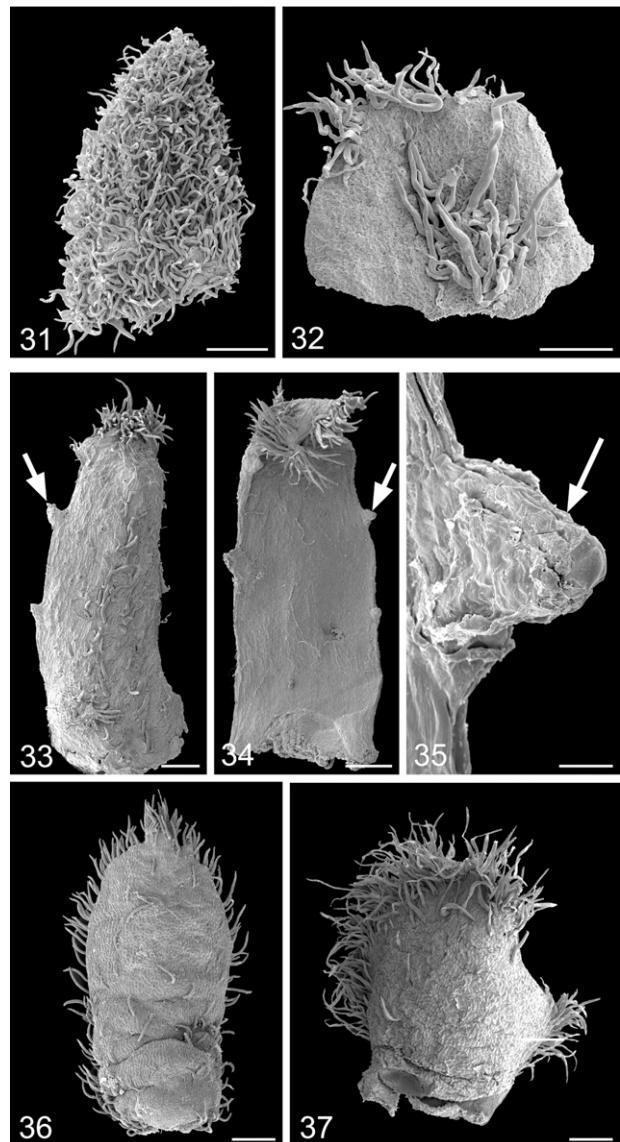


**Figures 29 and 30.** *Lophopyxis maingayi* (Lophopyxidaceae); male flowers with staggered anther dehiscence (arrows, smaller undehisced stamens; arrowhead, rudimentary gynoecium); from above. Figure 29. Bud with sepals removed. Figure 30. Entire anthetic flower with three dehisced and two undehisced stamens. Scale bars, 500 µm.

Pax (1890) found its position uncertain, probably not in Euphorbiaceae, possibly in Geraniales. It was transferred to Icacinaceae by Engler (1893) because of its climbing habit, similar to that of a few Icacinaceae. However, van Tieghem (1897) concluded, on the basis of ovule structure, that *Lophopyxis* did not belong to Icacinaceae and coined the informal name Lophopyxidacées. This view was repeated by Pierre (1897), who compared *Lophopyxis* with the genera of the current Cunoniaceae. Hallier (1910) placed *Lophopyxis* in Phyllanthoideae of Euphorbiaceae (see also Sleumer, 1942). It was formally placed in a separate family, Lophopyxidaceae, by Pfeiffer (1951) on the basis of floral structure and wood anatomy. [For a historical account, see also Sleumer (1968)]. Because of the isomerous flowers, Lophopyxidaceae was assumed to be somewhere in the Geraniales–Sapindales–Celastrales (Sleumer, 1971). Hutchinson (1959) and Cronquist (1981) placed *Lophopyxis* in Celastraceae, and Takhtajan (1987, 1997) placed Lophopyxidaceae in Celastrales. A position in Malpighiales, but outside Euphorbiaceae or Phyllanthaceae, was later supported by molecular studies (Savolainen *et al.*, 2000; APG II, 2003). In Savolainen *et al.* (2000), *Lophopyxis* was placed as sister to *Microdesmis* Hook.f. (Pandaceae).

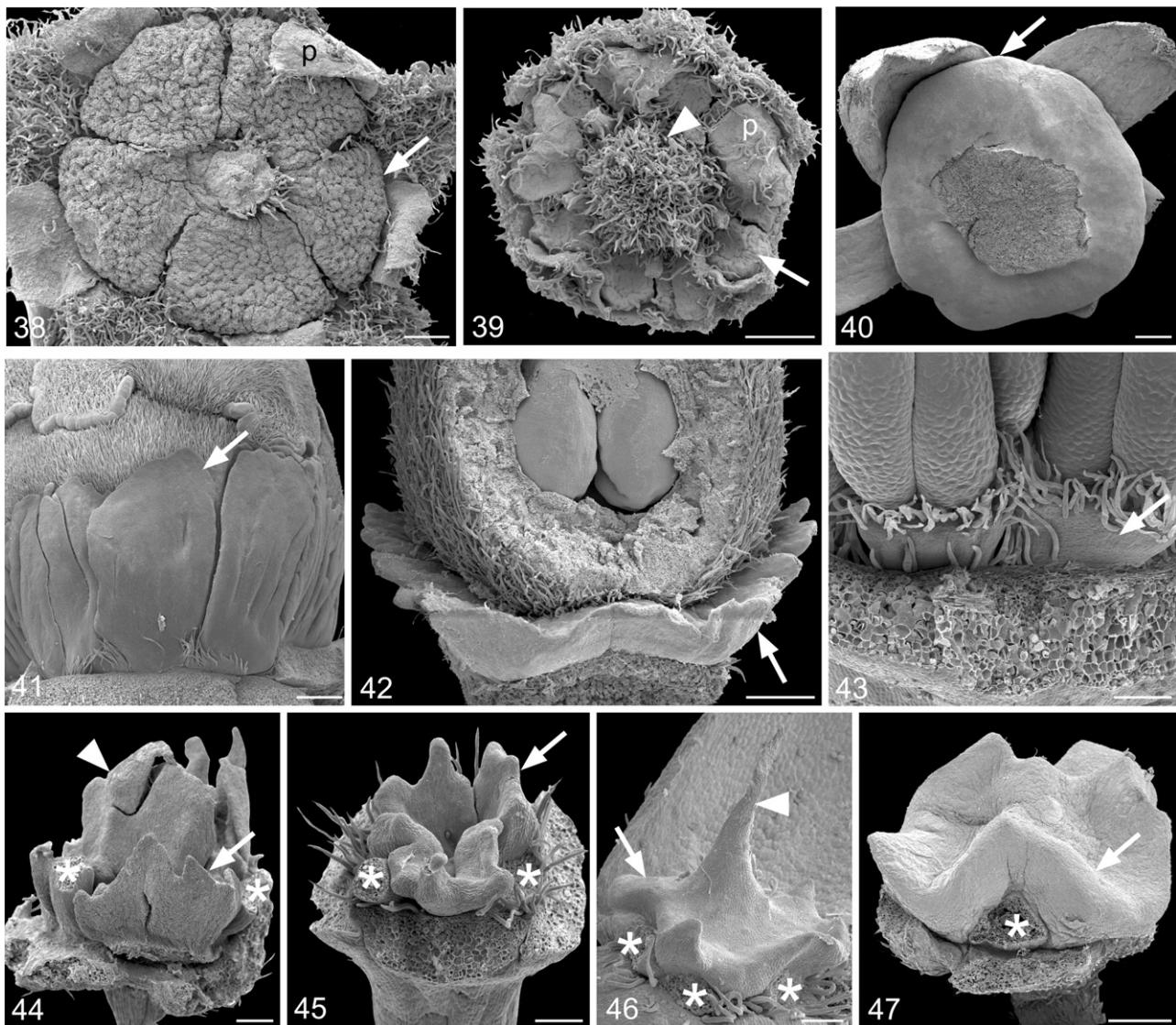
#### Putranjivaceae

Of the four genera, *Putranjiva*, *Drypetes*, *Sibangea* and *Lingelsheimia* Pax, often mentioned as belonging together (and treated in molecular phylogenetic analyses), only the first three are at present considered to be related. *Drypetes* was first described by Vahl (1807) without systematic placement. Endlicher (1836–1840) first used the suprageneric name Putranjiveae (including only *Putranjiva* and the unre-

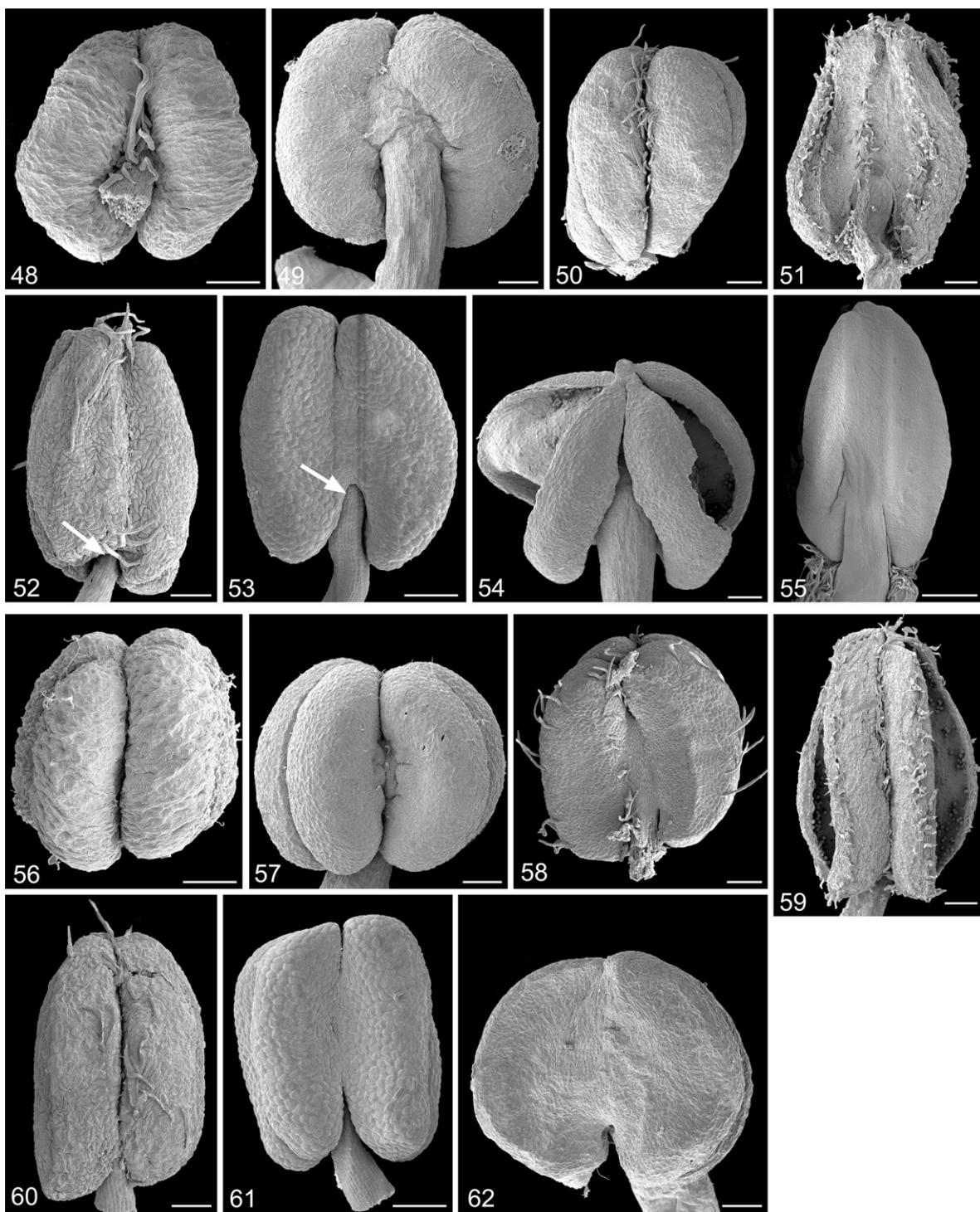


**Figures 31–37.** Perianth organs with hairs; buds (in Figure 36: anthesis). Figures 31 and 32. *Lophopyxis maingayi* (Lophopyxidaceae); female. Figure 31. Sepal, from dorsal. Figure 32. Petal, from dorsal. Figures 33–37. Putranjivaceae; sepals. Figures 33–35. *Sibangea arborescens*; male; sepals with glands (colleteres?) along margins. Figure 33. From dorsal. Figure 34. From ventral. Figure 35. Gland on sepal margin; from ventral. Figure 36. *Putranjiva roxburghii*; female; from dorsal. Figure 37. *Drypetes lateriflora*; female; from dorsal. Scale bars, 200 µm (Figs 31, 33, 34, 36, 37); 100 µm (Fig. 32); 20 µm (Fig. 35).

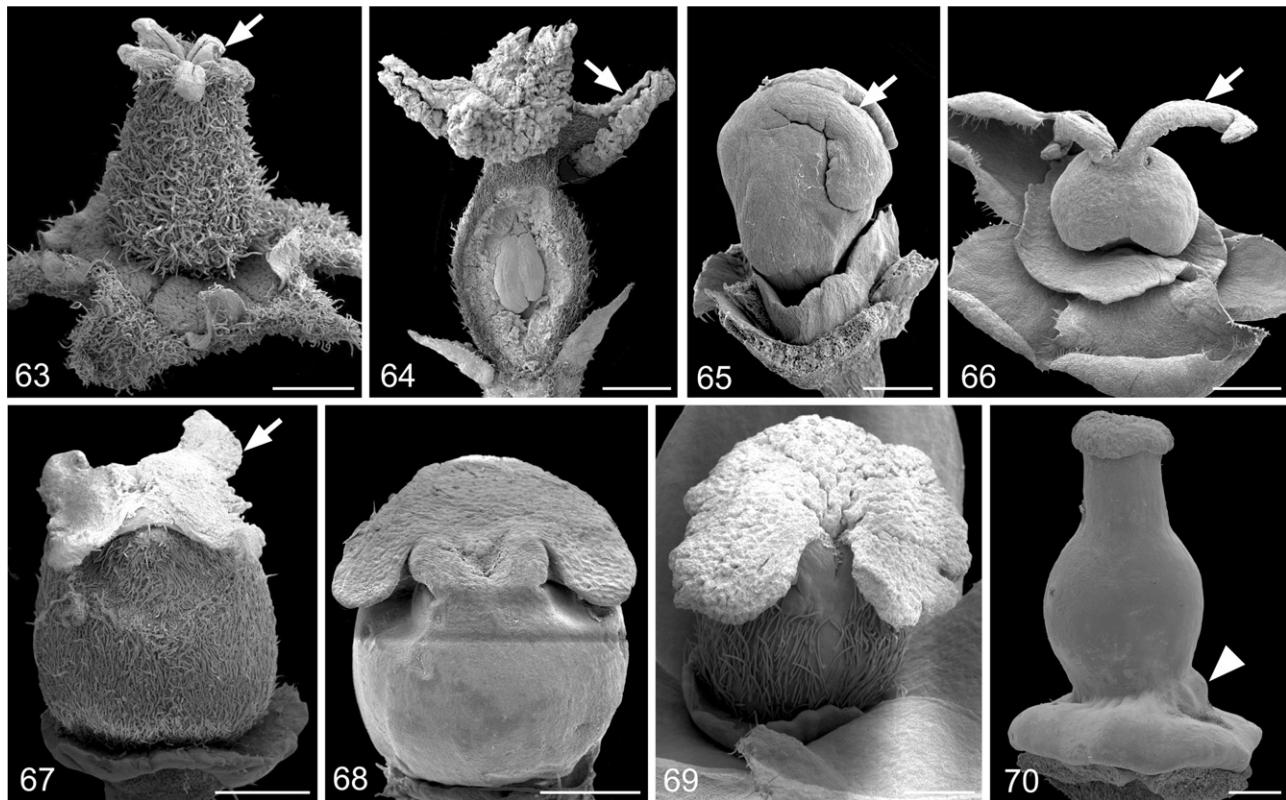
lated genus *Nageja*), but placed *Drypetes* in Buxea of Euphorbiaceae, and only Meisner (1842) gave a diagnosis for Putranjiveae. Bentham & Hooker (1883) treated *Putranjiva* and *Drypetes* (in proximity) in Phyllantheae of Euphorbiaceae. *Sibangea* was originally described under Phyllantheae of Euphorbiaceae



**Figures 38–47.** Flowers with nectaries (arrows: nectary; arrowhead: rudimentary gynoecium; asterisk: area of removed stamen). Figures 38 and 39. *Lophopyxis maingayi* (Lophopyxidaceae) (p, petal). Figure 38. Female flower at anthesis with large nectary lobes surrounding gynoecium (gynoecium removed); from above. Figure 39. Male bud; nectary lobes positioned to the inside of the stamens and a surrounding hairy rudimentary gynoecium; from above. Figures 40–47. Putranjivaceae. Figures 40–42. Female flowers. Figure 40. *Sibangea arborescens* (Putranjivaceae); flower at anthesis; nectary disc surrounding gynoecium (gynoecium removed); from above. Figure 41. *Drypetes gossweileri* (Putranjivaceae); bud (sepals removed); sinuously curved, flattened nectary surrounding base of gynoecium; antesepalous view. Figure 42. *Drypetes* sp. (Putranjivaceae); flower after anthesis with cup-shaped nectary surrounding gynoecium (sepals removed, ovary locule exposed); antesepalous view. Figures 43–47. Male flowers with nectary positioned inside the stamens; sepals and stamens removed (in Figure 43, only sepals removed; in Figure 46, only stamens removed). Figure 43. *Drypetes* sp. (Putranjivaceae); bud; nectary sinuously curving around the stamen bases; antesepalous view. Figure 44. *Drypetes madagascariensis* (Putranjivaceae); anthetic flower with pointed nectary lobes surrounding rudimentary gynoecium; antesepalous view. Figure 45. *Drypetes vernicosa* (Putranjivaceae); anthetic flower; antesepalous view. Figure 46. *Drypetes deplanchei* (Putranjivaceae); anthetic flower with nectary surrounding base of pointed rudimentary gynoecium; alternisepalous view. Figure 47. *Sibangea arborescens* (Putranjivaceae); advanced bud with nectary; antesepalous view. Scale bars, 200 µm (Figs 38, 39, 43–46); 500 µm (Figs 40–42, 47).



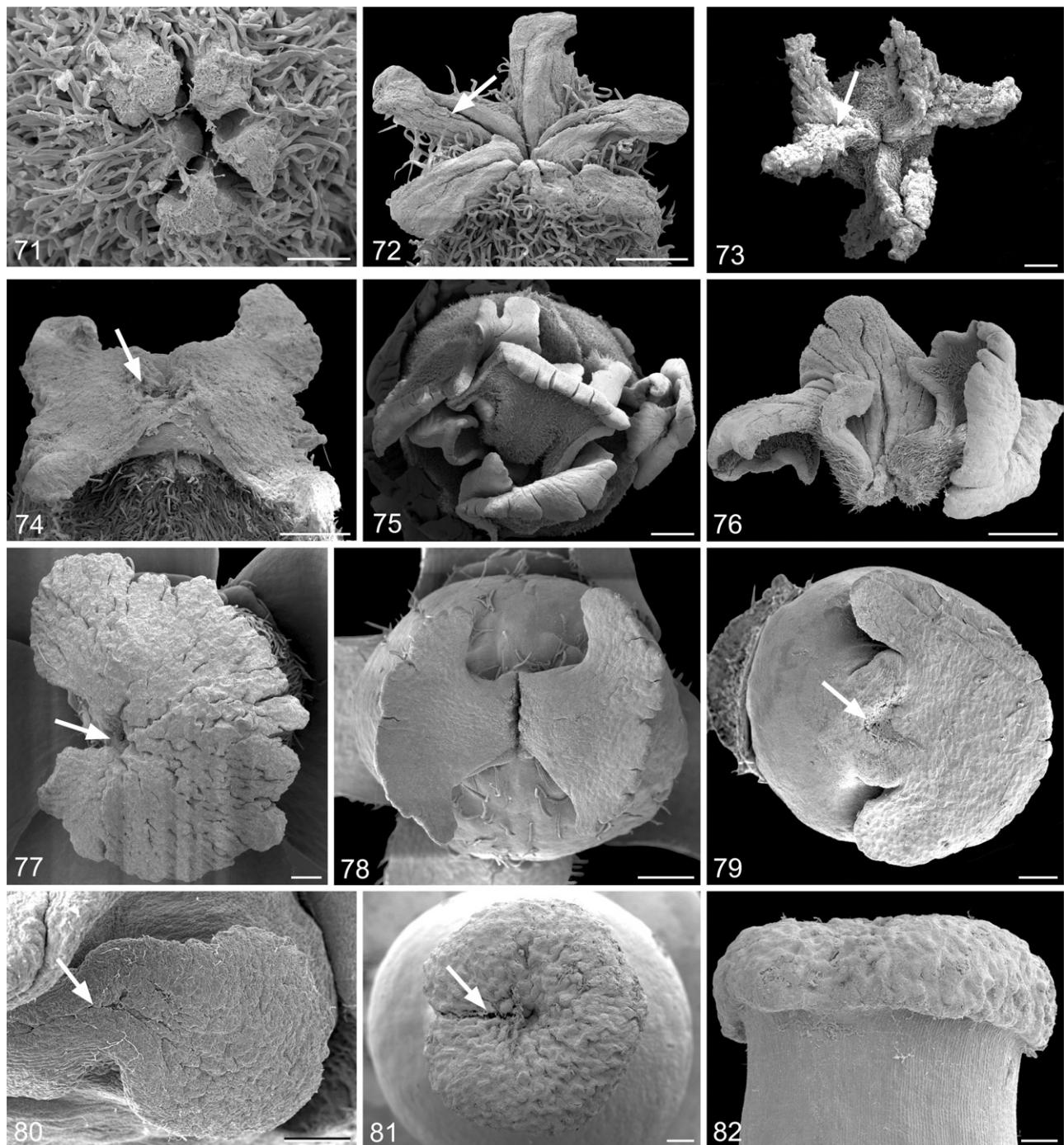
**Figures 48–62.** Stamens; male buds (in Figs 51, 54, 60, 62: anthesis). Figures 48–55. From dorsal. Figure 48. *Lophopyxis maingayi* (Lophopyxidaceae). Figures 49–55. Putranjivaceae. Figure 49. *Sibangea arborescens*. Figure 50. *Putranjiva roxburghii*. Figure 51. *Drypetes amazonica*. Figure 52. *Drypetes deplanchei*; upper part of filament in basal pseudopit (arrow). Figure 53. *Drypetes vernicosa*; upper part of filament in basal pseudopit (arrow). Figure 54. *Drypetes madagascariensis*. Figure 55. *Drypetes longifolia*. Figures 56–62. From ventral. Figure 56. *Lophopyxis maingayi* (Lophopyxidaceae). Figures 57–62. Putranjivaceae. Figure 57. *Sibangea arborescens*. Figure 58. *Putranjiva roxburghii*. Figure 59. *Drypetes amazonica*. Figure 60. *Drypetes deplanchei*. Figure 61. *Drypetes vernicosa*. Figure 62. *Drypetes madagascariensis*. Scale bars, 100 µm (Figs 48, 56); 200 µm (Figs 49–54, 57–62); 500 µm (Figure 55).



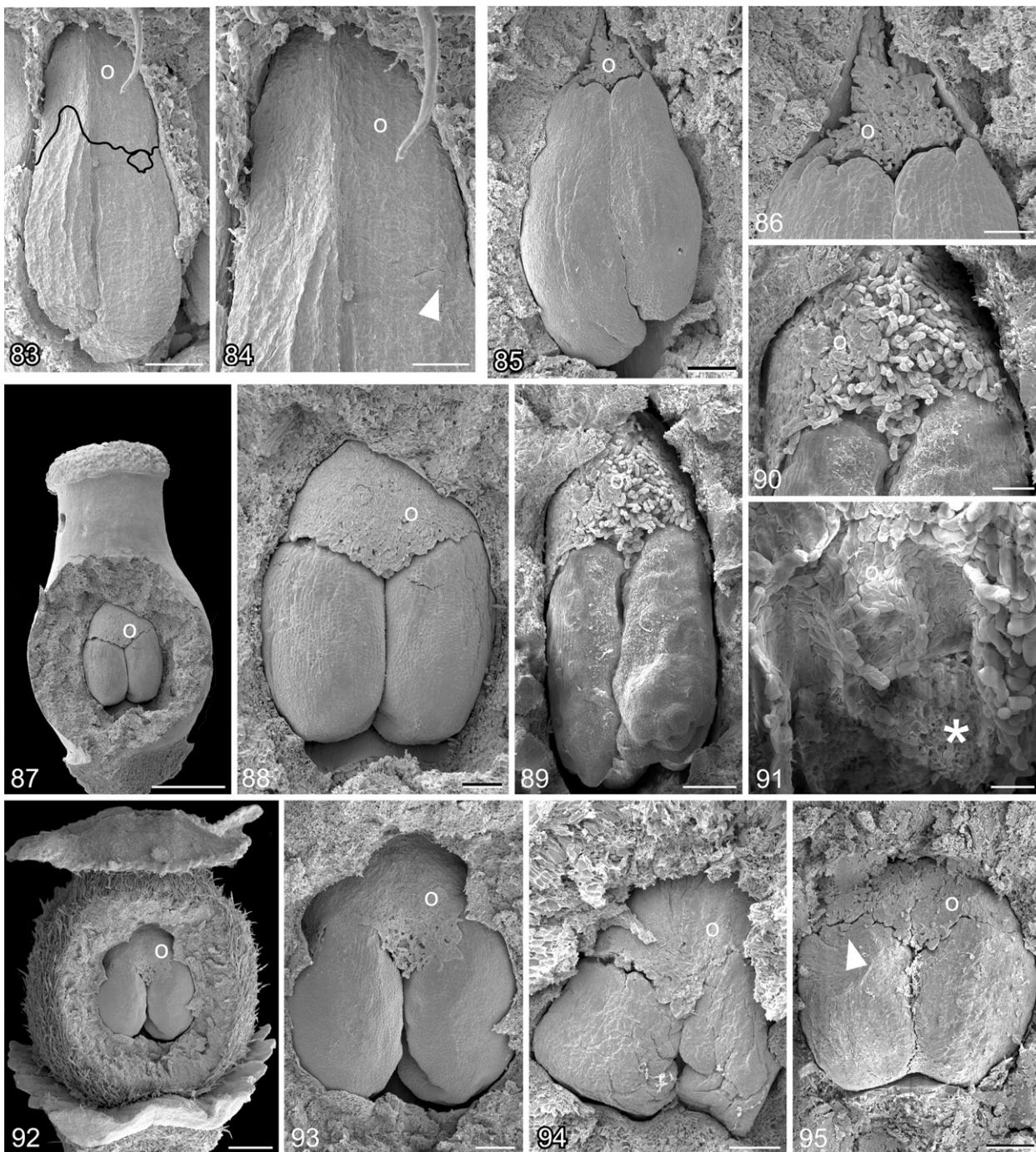
**Figures 63–70.** Gynoecia at anthesis from female flowers (in Figure 65: bud; in Figure 67: after anthesis; in Figures 65, 67, 68, 70: sepals removed); free parts of carpels reflexed (arrow, one carpel indicated). Figure 63. *Lophopyxis maingayi* (Lophopyxidaceae). Entire flower; antecarpellous view (pentamerous gynoecium). Figures 64–70. Putranjivaceae. Figure 64. *Putranjiva roxburghii*; locule of one carpel exposed; antecarpellous view (trimerous gynoecium). Figures 65 and 66. *Drypetes madagascariensis* (dimerous gynoecium). Figure 65. Bud with gynoecium from side; free parts of gynoecium folded over ovary. Figure 66. Alternicarpellous view. Figure 67. *Drypetes* sp.; alternicarpellous view (dimerous gynoecium). Figure 68. *Drypetes deplanchei*; gynoecium from ventral (unicarpellate). Figure 69. *Drypetes vernicosa*; gynoecium from ventral (unicarpellate). Figure 70. *Sibangea arborescens*; gynoecium from side (unicarpellate; ventral on right side) with potential remnant carpel(s) (arrowhead). Scale bars, 500 µm (Figs 63, 65, 68, 69); 1 mm (Figs 64, 66, 67, 70).

(Oliver, 1883), and was then included in *Drypetes* (Hutchinson, 1912), but later resurrected (without a discussion) (Radcliffe-Smith, 1976). In Pax & Hoffmann (1931), *Drypetes* and *Putranjiva* were treated in Phyllantheae, but in separate subtribes, Drypetinae and Glochidiinae (also, *Lingelsheimia* is in Drypetinae; *Sibangea* included in *Drypetes*). Punt (1962) recognized that the pollen of *Putranjiva* is ‘far more similar’ to that of *Drypetes* than to his ‘*Breynia* type’ (found in a subgroup of current Phyllanthaceae). *Drypetes* and *Putranjiva* appear together in a cladistic analysis of leaf structure (Levin, 1986). Webster (1994b) placed *Drypetes*, *Putranjiva* and *Sibangea* in Drypeteae (Phyllanthoideae). *Putranjiva* (= *Drypetes* s.l.) and Pandaceae form two separate lineages (not in Euphorbiaceae) based on *rbcL* (Wurdack & Chase, 1996); a separate family, Putranjivaceae, was used in

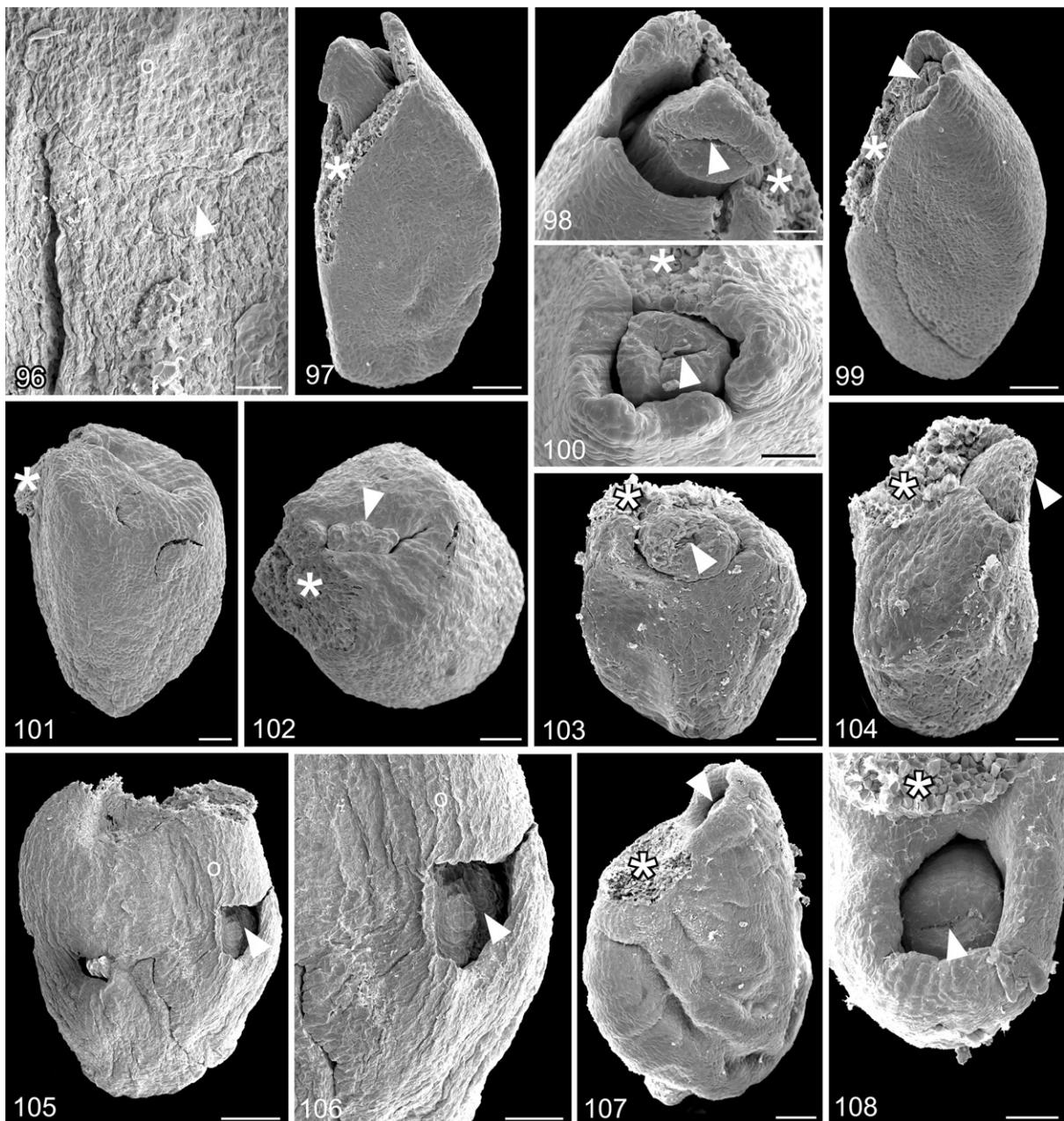
APG (1998) and was also supported by embryology (Tokuoka & Tobe, 1999). Putranjivaceae appeared as sister to Irvingiaceae (without support) in Savolainen *et al.* (2000). Among the other two genera believed to be close to *Drypetes*, *Sibangea* appears to be nested in *Drypetes* (with only weak support) (Wurdack *et al.*, 2004). In contrast, *Lingelsheimia* appears to be in Phyllantheae (Kathriarachchi *et al.*, 2005, 2006), as also indicated earlier by pollen and seed coat structure (Punt, 1962; Köhler, 1965; Webster, 1994b; Tokuoka & Tobe, 2001). However, a clear judgement of whether Putranjivaceae contains one, two or three genera (Pax & Hoffman, 1931; Webster, 1994b; Chakrabarty, Gangopadhyay & Balakrishnan, 1997) will only be possible when the results of additional molecular analyses are available, including a broader taxon sampling, especially with more *Drypetes* spp.



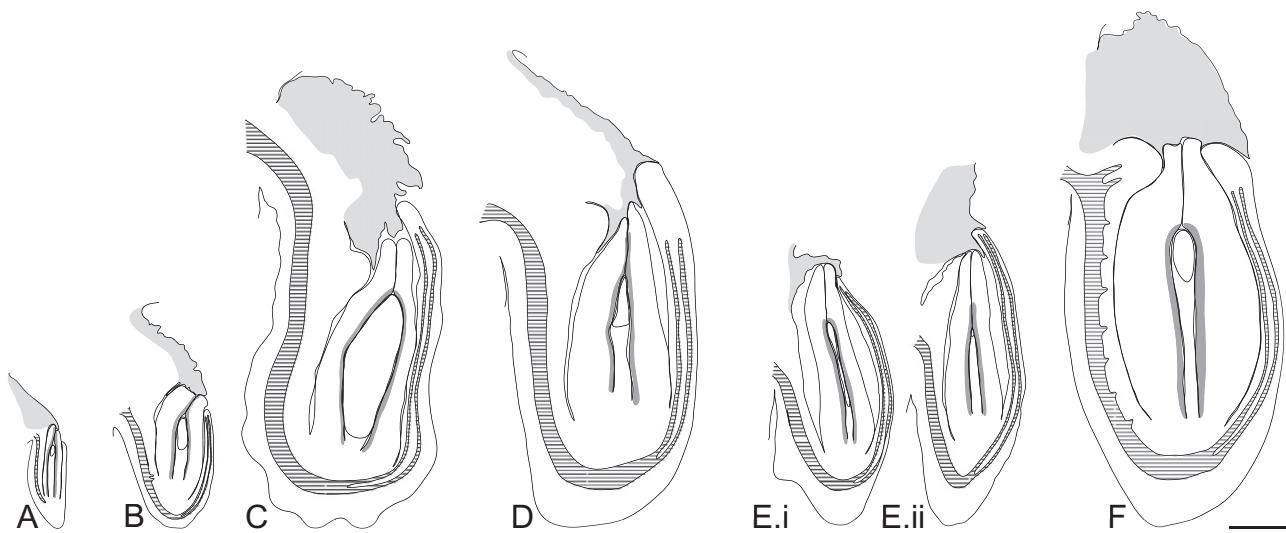
**Figures 71–82.** Stigmas from anthetic gynoecia of female flowers (in Fig 71: bud; in Figure 74: after anthesis; arrow, ventral slit). Figures 71 and 72. *Lophopyxis maingayi* (Lophopyxidaceae); punctiform stigmas. Figure 71. Gynoecium from above with upright carpel tips. Figure 72. Gynoecium with reflexed carpel tips. Figures 73–82. Putranjivaceae. Figure 73. *Putranjiva roxburghii*; branched stigmas from above. Figures 74–80. Gynoecia with large, flattened stigmas. Figure 74. *Drypetes* sp.; alternicarpellous view. Figures 75 and 76. *Drypetes gossweileri*. Figure 75. Gynoecium from above (some stigmas missing). Figure 76. Stigma of one carpel, from ventral. Figure 77. *Drypetes vernicosa*; from above. Figures 78 and 79. *Drypetes deplanchei*; from above. Figure 78. Bicarpellate gynoecium. Figure 79. Monocarpellate (pseudomonomerous?) gynoecium (ventral on left side of image). Figure 80. *Drypetes madagascariensis*. Figures 81 and 82. *Sibangea arborescens*; stigma capitate. Figure 81. From above. Figure 82. Stigma from ventral. Scale bars, 100 µm (Figure 71); 200 µm (Figs 72, 77, 79–82); 500 µm (Figs 73, 74, 78); 1 mm (Figs 75, 76).



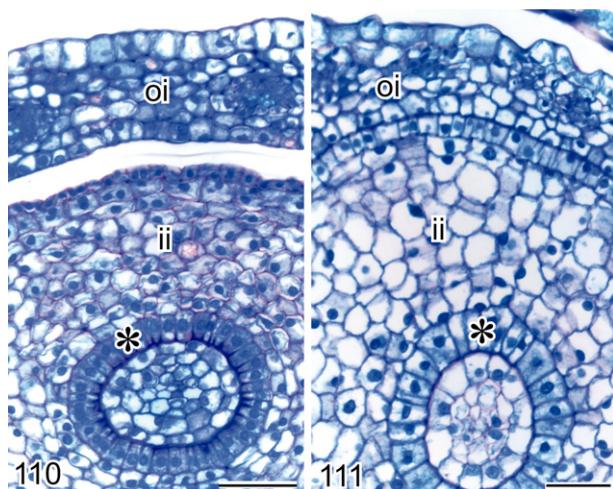
**Figures 83–95.** Locules with obturators and two collateral antitropous ovules; anthetic female flowers (in Figures 92–94: after anthesis); o, obturator; arrowhead, micropyle. Figures 84, 86, 90, 91. Close up of obturators and upper part of ovules (in Figure 91: obturator only, ovules removed). Figures 83 and 84. *Lophopyxis maingayi* (Lophopyxidaceae). Figure 83. Lower margin of obturator and outline of inner integument indicated by black lines. Figure 84. Detail of Figure 83 in higher magnification. Figures 85–95. Putranjivaceae. Figures 85 and 86. *Putranjiva roxburghii*; ovule with lobed outer integument. Figures 87 and 88. *Sibangea arborescens*. Figure 87. Entire gynoecium with locule exposed. Figures 89–91. *Drypetes gossweileri*. Figure 91. Obturator; its surface showing the imprint left behind by the upper part of the ovule (ovule removed) (asterisk, attachment region of ovule). Figures 92 and 93. *Drypetes* sp. Figure 92. Gynoecium with locule exposed. Figure 94. *Drypetes madagascariensis*. Figure 95. *Drypetes deplanchei*. Scale bars, 100 µm (Figs 83, 86, 90, 94, 95); 50 µm (Figs 84, 91); 200 µm (Figs 85, 88, 89, 93); 1 mm (Figure 87); 500 µm (Figure 92).



**Figures 96–108.** Ovules with micropyle formed by the inner integument; from female flowers at anthesis (asterisk, attachment region of ovule; arrowhead, inner integument in region of micropyle; o, obturator). Figures 96–98, 101–104. Inner integument longer than outer. Figures 99, 100, 105–108. Inner integument shorter than outer integument, but outer integument not directly involved in micropyle formation as its entrance is widely open. Figure 96. *Lophopyxis maingayi* (Lophopyxidaceae). Obturator and upper part of ovule. Figures 97–108. Putranjivaceae. Figures 97–100. *Putranjiva roxburghii*. Figure 97. Ovule from side. Figure 98. Same ovule from other side showing protruding inner integument and transverse slit-like micropyle. Figure 99. Ovule from side. Figure 100. Micropylar region of same ovule, with lobed integuments, from above. Figures 101 and 102. *Sibangea arborescens*. Figure 101. Ovule from side. Figure 102. Same ovule; from above. Figures 103 and 104. *Drypetes deplanchei*. Figure 103. Ovule from above. Figure 104. Same ovule from side. Figures 105 and 106. *Drypetes lateriflora*. Ovules plus obturators; outer integument of ovules forming a window-like hole in which the inner integument is housed. Figure 106. Close up of inner and outer integument. Figures 107 and 108. *Drypetes gossweileri*. Figure 107. Ovule from side. Figure 108. Micropylar region from above; micropyle formed by transverse slit. Scale bars, 20 µm (Figure 96); 100 µm (Figs 97, 99, 101, 102, 105, 107); 50 µm (Figs 98, 100, 103, 104, 106, 108).



**Figure 109.** Schematic median longitudinal sections of anthetic or slightly post-anthetic ovules and obturators (shaded light grey) from female flowers; embryo sac and vascular bundle indicated by thin lines (vascular bundles also with dash-pattered interior); endothelium shaded dark grey. A, *Lophopyxis maingayi* (Lophopyxidaceae). B–F, Putranjivaceae. B, *Drypetes deplanchei* (endothelium only weakly differentiated). C, *Drypetes gossweileri*. D, *Drypetes* sp. E, *Putranjiva roxburghii*. E.i, Outer integument shorter than inner integument. E.ii, Outer integument longer than inner integument. F, *Sibangea arborescens*. Scale bar, 200 µm.



**Figures 110–111.** Putranjivaceae. Transverse microtome sections of ovules with endothelium from female flowers at level below embryo sac (oi, outer integument; ii, inner integument; asterisk, endothelial layer). Figure 110. *Drypetes* sp. (post-anthetic). Figure 111. *Sibangea arborescens* (anthetic). Scale bars, 50 µm.

#### FLORAL STRUCTURE OF LOPHOPYXIDACEAE AND PUTRANJIVACEAE

##### Flower size, shape, merism, symmetry, sex distribution and floral biology

The flowers are mostly small. They are simple, plate-like, with widely open or upright (or reflexed) perianth

organs. A floral cup is present in *Lophopyxis* (Figs 1, 2), female *Sibangea* (Fig. 16) and in some *Drypetes*. A basally weakly articulated pedicel was seen in female *Sibangea*, some *Drypetes* and female *Putranjiva*, but not in *Lophopyxis*. The flowers are mostly tri- to pentamerous (*Lophopyxis*, Fig. 1; *Putranjiva*, Figs 13–15; some *Drypetes*, Fig. 10), with few exceptions of fewer or more organs, especially in the androecium with numerous stamens (from three to 50) in some *Drypetes* spp. (Pax & Hoffmann, 1921; Forster, 1997), and in the gynoecium with only one or two fertile carpels in *Sibangea* (Fig. 17) and some *Drypetes* (Fig. 5) (but also up to six and more in *Drypetes*) (Putranjivaceae). The flowers are polysymmetric. They are always functionally unisexual. Functionally male flowers have a reduced gynoecium (except for *Putranjiva*) (Figs 39, 44, 46), but functionally female flowers do not have androecium rudiments. They are monoecious in *Lophopyxis* (Sleumer, 1971), but commonly dioecious in Putranjivaceae (Pax & Hoffmann, 1931). Floral biology is poorly known. The flowers are in general inconspicuous. However, they have prominent nectaries in both families (Figs 38–47), except for *Putranjiva*, in which nectaries are lacking (and which is probably wind pollinated).

##### Calyx

A calyx is always present. Synsepaly occurs for a short distance in Putranjivaceae and irregularly, only in part of the sepals of a flower, in *Lophopyxis*. The

sepals are short and form protective organs only in young buds in female *Lophopyxis*, *Putranjiva* and female *Sibangea* and a few *Drypetes* (Figs 19–24), in contrast with male *Lophopyxis*, most *Drypetes* and male *Sibangea*, where they are also protective in older buds (Figs 25–28). Aestivation is quincuncial in pentamerous calyces (*Lophopyxis*, *Drypetes p.p.*, *Sibangea*) (this study; Léandri, 1958) or open (female *Lophopyxis*, *Putranjiva*). In male *Sibangea*, the sepal tips are quincuncial but, because the sepals have a narrow middle zone (above the synsepalous zone), the aestivation is open at this level (Fig. 18). It is decussate in tetramerous calyces (*Drypetes p.p.*) (Fig. 4). Sepals have a pointed (*Lophopyxis*, *Putranjiva*, female *Sibangea*) (Figs 31–37) or a rounded (*Drypetes*, male *Sibangea*) apex. The sepals of a flower have different sizes, the outer ones tending to be shorter (Fig. 28). In female flowers, sepals tend to abscise after anthesis (in *Putranjiva* and some *Drypetes*). In male flowers of *Lophopyxis*, each sepal enwraps a stamen (Fig. 3A). The sepal margins are fringed (or partially fringed) in Putranjivaceae, but not in Lophopyxidaceae, although the sepals are densely covered with hairs (Figs 31, 33, 34, 36, 37). The sepals have three vascular traces in *Lophopyxis*, *Sibangea* and *Drypetes*, but a single trace in *Putranjiva*.

#### *Corolla*

A corolla is lacking in Putranjivaceae. In contrast, five petals, although small and inconspicuous, are present in Lophopyxidaceae (Figs 32, 38, 39). They have an open aestivation with a narrow base and a broad blade, and a single vascular trace.

#### *Androecium*

Stamens are only present in male flowers; in female flowers, not even stamen rudiments occur. Haplostemony with the stamens antesepalous is present in *Lophopyxis* (Fig. 3). In *Putranjiva* (Fig. 15), *Sibangea* (Fig. 18) and *D. madagascariensis* (Fig. 10), which have more sepals than stamens, it appears that the one, two or three outermost sepals are associated with a stamen in the same radius. Thus, there is an antesepalous position for the first organs. Diplostemony occurs in some *Drypetes* spp. However, in other species, the position is more irregular as the number of stamens is variable. Some *Drypetes* spp. are polystemonous [up to 50 stamens in *D. longifolia* (Blume) Pax et K. Hoffm.; Pax & Hoffmann, 1921]; many are in the range of 8–20; c. 10% of the species do not have more than four or five stamens (Pax & Hoffmann, 1921). The species studied here have three (*D. madagascariensis*), c. seven (*D. deplanchei*) and c. 40 (*D. gossweileri*, Fig. 9) stamens. A low number of stamens (five or three) may be ancestral in the clade of the two families. However, as long as the sister of

this clade has not been determined and as the internal topology of *Drypetes* is unknown, this is not certain. Stamens are free or only shortly united (the latter in *Putranjiva* and an undetermined *Drypetes* species connected via the nectary, Fig. 12). The filaments are longer than the anthers at anthesis (except for *D. deplanchei*, where they remain shorter). The anthers are basifixated in *Lophopyxis*, *Putranjiva* and partly in *Drypetes*, but slightly dorsifixated in some other *Drypetes* spp. and *Sibangea* (Figs 48–62). They are nonversatile (except *D. gossweileri*). The anthers are mostly latrorse or extrorse (but introrse in *D. deplanchei*), introrse to latrorse in *Sibangea*; they are mostly 'X' shaped. A connective protrusion was only seen in *D. madagascariensis*. Each anther dehisces with two lateral longitudinal slits, which are not continuous over the apex. The septum between the two pollen sacs of each theca is broad and persists after dehiscence in *Putranjiva*. The endothecium does not extend over the dorsal and ventral sides of the connective (except for *D. madagascariensis* among the species studied), and is not continuous behind the thecae (for this feature in rosids, see Endress & Stumpf, 1991).

#### *Gynoecium*

*Lophopyxis* has five (or four) carpels (this study; Sleumer, 1971) (Fig. 3). In Putranjivaceae, *Putranjiva* has three carpels (Fig. 14), most *Drypetes* spp. have two carpels (Fig. 11), but a few species have three or four, and a singular exception is *D. gossweileri* (= *D. armoracia* Pax & K.Hoffm.) with six or seven carpels (this study, Fig. 8; Pax & Hoffmann, 1921; Brenan, 1952; Hutchinson & Dalziel, 1954). Gynoecia of *Sibangea* and some *Drypetes* spp. [section *Hemicyclia* (Wight & Arn.) Pax & K.Hoffm.] have a single locule (Figs 5, 17). The question is whether these gynoecia are monomerous (with a single carpel) or pseudomonomerous (with a single fertile carpel and one or more additional, highly reduced carpels). This question will be considered at the end of this section, after discussion of the general properties of the gynoecia. The ovary is superior in all genera. The gynoecium is syncarpous up to the mid- to upper style in both families. The ovary is synascidiate up to above the placenta, and thus the placenta is axile. The ovary is septate throughout in gynoecia with more than one carpel. Only in *Putranjiva* is it unilocular in the symplicate zone (Fig. 14). An apical septum is present in the ovary of *D. gossweileri* (Fig. 8E). In some *Drypetes* spp., the styles are short and thus the stigmas are almost sessile (Figs 67–69). Stigmatic branches are bifurcate in *Putranjiva* (Fig. 73), but not in the other genera [but bilobed in *D. macrophylla* (Blume) Pax & K. Hoffm., according to Pax & Hoffmann (1921), and multi-lobed in *D. gossweileri*;

this study]. They are reflexed at anthesis (not in *Sibangea* with a capitate stigma) (Figs 66–69, 72–80). The stigmas are nonpapillate, except for *Putranjiva*, which has multiseriate pluricellular protuberances (Fig. 73). The carpel tips are closed in bud in *Lophopyxis* (Fig. 71), but not in Putranjivaceae. Angiospermy type 2 (Endress & Iggersheim, 2000) is present in all genera, but type 4 is present in some *Drypetes* spp. A short stylar canal in individual carpels is present in *Putranjiva* and *Sibangea*. A gap in the centre of the symplicate zone is present in *Lophopyxis*, *Putranjiva* and some *Drypetes* spp., and is especially well developed in the multicarpellate gynoecium of *D. gossweileri* (Fig. 8). The ventral carpel slit extends into the stigma in *Sibangea* (Fig. 81), but ends below the stigma in *Lophopyxis* and other Putranjivaceae (Figs 72, 77, 79, 80). Downwards it extends as a postgenitally fused ventral furrow into the synascidiate zone in all genera, except for *Putranjiva*. PTTT is restricted to the inner angle of the ventral slit in the plicate and upper symplicate zone of *Lophopyxis* (Fig. 2), but is also present in its flanks in Putranjivaceae and lower down in *Lophopyxis* (Fig. 2). The compitum extends throughout the symplicate zone in *Lophopyxis* and Putranjivaceae with more than one carpel (Figs 8, 11, 14). A (short) gynophore is present in all genera. In male flowers, a rudimentary gynoecium without ovules is present (except *D. gossweileri*) (Figs 39, 44, 46). It is still syncarpous with a short synascidiate zone in *Lophopyxis*, but is mostly not syncarpous and lacks an inner surface in Putranjivaceae (but with an inner surface in *D. gossweileri*).

With respect to the question of the morphology of the unilocular gynoecia with just two ovules in *Sibangea* and part of *Drypetes*, there are indications that they are pseudomonomerous and not monomerous. These indications include the following.

1. The gynoecium is congenitally closed up to part of the style. The same is true in gynoecia with two or more fertile carpels. If the gynoecium were truly monomerous, one could expect that the ventral slit would reach down to just above the placenta, as in the syncarpous gynoecia of the species with two or more fertile carpels.
2. The ovary wall on the side of the placenta (ventral side of the fertile carpel) tends to be somewhat thicker than on the opposite side (dorsal side), and tends to contain more series of vascular bundles (Figs 4D, 5H, 16C, 17H) than the dorsal side. This indicates that (at least) one solid sterile carpel may be incorporated in the ovary wall of the ventral side of the fertile carpel.
3. If the ovary is reduced to a single locule, there can still be three stigmas in *Drypetes* (Michaelis, 1924).

4. It is a general feature that, in syncarpous clades, gynoecia reduced to a single locule tend to be pseudomonomerous (and not monomerous), as shown in a number of families in eudicots and monocots (e.g. Eckardt, 1937; Müller-Dobties, 1970; Schönenberger & Endress, 1998; Endress, 2002, 2011b; Ronse Decraene, Linder & Smets, 2002; Matthews & Endress, 2004, 2008; Bachelier & Endress, 2007; González & Rudall, 2010; Tobe, 2011).

Thus, we would conclude that the gynoecia studied here with only one locule are most likely pseudomonomerous; however, developmental studies are needed to confirm this.

#### Ovules

In each carpel, there are two collateral antitropous (epitropous) pendant ovules with the micropyles facing upwards, and each with a large obturator, in all taxa studied of both families (Figs 83–90, 92–95, 105). The ovules are anatropous and bitegmic (Fig. 109). According to Corner (1976), the ovules of *D. macrostigma* J.J.Sm. are unitegmic with the inner integument lost. The ovules have long and conspicuously slender nucelli and are either weakly crassinucellar or incompletely tenuinucellar (for *Lophopyxis*, see also personal communication by Mauritzon in Sleumer, 1942; for *Putranjiva*, see also Banerji & Dutt, 1944; Thathachar, 1953; Singh, 1970). However, *Putranjiva* has two parietal cell layers (Thathachar, 1953; Tokuoka & Tobe, 1999), not one, and is thus technically crassinucellar (following the classification of Endress, 2011a). There is neither a nucellar cap nor a nucellar beak (see also Tokuoka & Tobe, 1999). The ovules have an endothelium (Figs 110, 111) and the nucellus disintegrates around the embryo sac in all species studied (for *Putranjiva*, see also Thathachar, 1953; Singh, 1970) (Fig. 109). The presence of an endothelium at anthesis is still expressed in the seed coat in all three genera of Putranjivaceae (Stuppy, 1996). The inner integument is thicker than the outer (e.g. Figs 110, 111). In *Lophopyxis*, the outer integument is three cell layers thick, the inner five or six. In *Drypetes*, they are three to seven and five to nine cell layers thick, respectively, in *Sibangea* five and seven or eight and, in *Putranjiva*, four or five and five to eight. Only in *D. gossweileri* are both integuments equally thick with five or six cell layers. The outer integument is semi-annular and both integuments are lobed in all species studied (Fig. 100). In Putranjivaceae, two lobes of the outer integument regularly form a lateral slit. The slits of the two collateral ovules in a carpel either face each other (some *Drypetes* spp.) or are directed away from each other

(*Putranjiva*, *Sibangea*). There is a gap between the integuments in *Putranjiva* and some *Drypetes* spp. (Figs 98, 105, 106, 108). The raphe forms a somewhat elevated ridge in *Putranjiva* and some *Drypetes* species. A long micropyle is present in both families. It is formed by the inner integument (Figs 96, 100, 103, 108, 109) and may take the form of a transverse slit (Figs 98, 103, 108) in some Putranjivaceae. According to Tokuoka & Tobe (1999), there is some lability, with micropyles formed by the inner integument or by both integuments in both *Drypetes* and *Putranjiva*. However, in the material of our study, the outer integument was never involved directly in micropyle formation, except that, in some species, it formed, together with the obturator, a narrow slit as passageway for pollen tubes before they reach the micropyle. The rim of the inner integument is sloping, as the integument is shorter on the antiraphal side than on the raphal side, in *Lophopyxis* (Fig. 96), *Sibangea* (Fig. 101) and some *Drypetes* spp. (Figs 103, 104). In *Putranjiva*, *Sibangea* and some *Drypetes* spp., the obturator protrudes into the ovule between the two integuments or, more rarely, via the micropyle (Fig. 109). Branches of the ovular bundle extend from the chalaza into the outer integument in all Putranjivaceae studied (for some Putranjivaceae, see also Singh, 1970; Corner, 1976; Stuppy, 1996). However, there are no vascular bundles in the integuments of *Lophopyxis*.

#### Nectaries

Nectaries are present in both families, except for *Putranjiva* (Figs 38–47). In *Lophopyxis*, there are five large lobes alternating with the sepals (Figs 38, 39). However, in most Putranjivaceae, the nectary has the shape of a relatively thin sheet or cup around the gynoecium (in male flowers, around the rudimentary gynoecium) (Figs 40–47). The nectary is also lobed in *D. madagascariensis* with three lobes alternating with the three outer sepals (Figs 10, 44). In *Lophopyxis*, each nectary lobe arises from the base of a petal. The nectary partly covers the base of the petals (*Lophopyxis*) (Figs 1, 3, 38) or the base of the stamens (*Drypetes*, Figs 45, 46; *Sibangea*, Fig. 47). The nectary lines, in addition, the inner surface of the floral cup in *Lophopyxis*, *Sibangea* and some *Drypetes* spp. In *Drypetes*, the nectary often has a sinuous collar-like shape surrounding each stamen from the inside (see also figures in Hutchinson & Dalziel, 1954; Radcliffe-Smith, 1990; Tokuoka & Peng, 1997) (Fig. 12), whereas, in female flowers, it often forms a disc surrounding the gynoecium, often with a thin rim (Figs 42, 65, 66). The nectaries are supplied by mainly phloematic vascular bundles, which connect with sepal, petal or carpel bundles.

#### Histology

There is an abundance of hairs in the flowers of both families. In Putranjivaceae, both unicellular and multicellular lignified hairs occur, whereas, in *Lophopyxis*, only unicellular lignified hairs were found. An abundance of tanniferous tissue occurs in Lophopyxidaceae, whereas only little is present in Putranjivaceae and, when present, is mostly associated with the vasculature. Mucilage cells and special mucilage cells (as defined in Matthews & Endress, 2006) were not found in either family. Hairs in ovary locules were only found in the reduced and incompletely closed gynoecium of functionally male flowers of *Lophopyxis*. Sclerenchymatic tissue was found in the gynoecium of *Putranjiva* and some *Drypetes* spp. Cells with oxalate druses occur in various organs in all taxa studied, for instance, in *Lophopyxis*, they are concentrated in the centre of the septate ovary. Cells with raphides in the anthers were only found in *Lophopyxis*. Stomata occur in all genera, mainly on the dorsal side of the sepals (in some taxa raised), but sometimes also on the gynoecium. On the nectary, they were only seen in *Lophopyxis* and *Sibangea*.

#### Fruits

Fruits are nondehiscent and are differentiated as drupes, in *Lophopyxis* with wings (Webster, 1994b).

#### FLORAL STRUCTURE AND SYSTEMATICS

##### *Comparison of the three genera of Putranjivaceae*

The three genera are all similar in their floral structure. The distinction between *Sibangea* and *Drypetes* was emphasized by Radcliffe-Smith (1976). However, the difference between *Sibangea* and *Drypetes*, consisting in open versus imbricate sepals in female buds (Webster, 1994b), cannot be upheld (this study). The sepals are also imbricate in young female buds in *Sibangea*. Further, the sepals are persistent in fruit not only in *Sibangea* (Webster, 1994b), but also in some *Drypetes* spp. (this study). However, they have distinctly different shaped stigmas (capitate in *Sibangea* vs. dorsoventrally flattened lobes in *Drypetes*; bifurcate and, on average, larger in *Putranjiva*). The gynoecium has a single fertile carpel in *Sibangea* and some *Drypetes* spp. (probably pseudomonomerous in both genera). Functionally male flowers have a reduced gynoecium in *Drypetes* and *Sibangea*, but not in *Putranjiva*, where it is completely absent. *Drypetes* and *Sibangea* have a nectary disc, but *Putranjiva* does not. The ovary is unilocular in the symplicate zone in *Putranjiva*, but not in the other genera. The stigma is nonpapillate, but multicellular-papillate in *Putranjiva*. The greater differences in floral structure

between *Putranjiva* and the other two genera may be a consequence of modifications as a result of its wind pollination.

*Comparison of Lophopyxidaceae (L) and Putranjivaceae (P)*

The listed shared features between Lophopyxidaceae and Putranjivaceae support their close relationship (features of special interest in bold). The differences show their independent status.

Similarities

1. **Flowers unisexual, male flowers with reduced gynoecium, but female flowers without androecium rudiments.**
2. Calyx shortly synsepalous.
3. **Sepals not protecting gynoecium in older buds** (thus flowers ‘open’).
4. **Outer sepals tend to be shorter than the inner ones.**
5. **Petals small or lacking.**
6. Stamens antesepalous (*Lophopyxis*; in *Putranjiva*, *Sibangea* and some *Drypetes*, at least the outermost sepals are associated with a stamen).
7. Anthers ‘X’ shaped.
8. **(Short) gynophore present.**
9. Ovary superior.
10. Gynoecium syncarpous up to the mid- to upper style.
11. Synascidiate zone extending up to above the placenta and obturators located in the symplicate and uppermost synascidiate zone.
12. Stigma nonpapillate (but *Putranjiva* with multicellular protuberances and *Sibangea* with irregular ridges).
13. **Ventral carpel slits extending downwards into the synascidiate zone as postgenitally fused ventral furrows** (except for *Putranjiva*).
14. **Compitum extending throughout symplicate zone** (in Putranjivaceae in all species that have more than one carpel).
15. **Broad dorsal band of vascular bundles present in the style.**
16. **Two collateral antitropous ovules per carpel present, with obturator.**
17. **Ovules only weakly crassinucellar or incompletely tenuinucellar.**
18. **Endothelium present.**
19. Nucellus long and conspicuously slender.
20. Nucellar cap or nucellar beak lacking.
21. **Micropyle present.**
22. Nectary lobes (when present) alternating with the (outer) sepals.
23. Pedicel articulation weak or lacking (in contrast

with many other Malpighiales; Stevens, 2001 onwards; Matthews & Endress, 2008, 2011; Matthews *et al.*, 2012).

**24. Fruit indehiscent.**

25. Mucilage cells and special mucilage cells (as defined by Matthews & Endress, 2006) absent in floral organs.

Differences

1. Monoecy (L; see also Sleumer, 1971) vs. dioecy (P, mostly; Pax & Hoffmann, 1931).
2. Gynoecium in male flowers small, but still syncarpous with a rudimentary synascidiate zone (L) vs. more reduced, commonly not syncarpous, and without internal space (P, but *D. gossweileri* with inner surface and reduced ovules).
3. Flowers isomerous (L) vs. anisomerous (P).
4. Sepal margins not fringed (L) vs. fringed (or partially fringed, *Sibangea*) (P).
5. Petals present (L) vs. absent (P).
6. Carpel tips closed in bud (but reflexed at anthesis) (L) vs. not closed in bud (P).
7. Outer surface of the ovary wall with vertical ridges (L) vs. without vertical ridges (P).
8. Stigma small (L) vs. large (P).
9. PTTT restricted to the inner angle of the ventral slit (L) vs. not restricted (P).
10. Vascular bundles lacking in integuments (L) vs. present in outer integument (P).
11. Tanniferous tissue abundant in all floral organs (L) vs. not abundant (P).

*Comparison of Lophopyxidaceae and Putranjivaceae with Euphorbiaceae s.l. without Putranjivaceae (current Euphorbiaceae, Phyllanthaceae, Picrodendraceae and Peraceae; see Glossary)*

Here, we list apparent similarities and differences between Lophopyxidaceae/Putranjivaceae and Euphorbiaceae *s.l.* However, many of the listed similarities are floral reductions and may be seen as separate autapomorphies for Lophopyxidaceae/Putranjivaceae and families of Euphorbiaceae *s.l.* In addition, a number of similarities are also shared with other Malpighiales (see below), and may therefore represent plesiomorphies or apomorphic tendencies in Malpighiales. The listed differences between Lophopyxidaceae/Putranjivaceae and Euphorbiaceae *s.l.* are shared, instead, by Lophopyxidaceae/Putranjivaceae and other Malpighiales (see below), and thus support more distant relationships with Euphorbiaceae *s.l.* Rafflesiaaceae is not added to this list, although it is sister to Euphorbiaceae *s.s.* (Davis *et al.*, 2007; Wurdack & Davis, 2009), because it is extremely autapomorphic.

## Similarities

1. Flowers unisexual: Lophopyxidaceae, all Putranjivaceae – almost all Euphorbiaceae *s.l.* (Pax & Hoffmann, 1931).
2. Flowers trimerous: *Putranjiva* (except calyx), some *Drypetes* and *Sibangea* (only androecium) – many Euphorbiaceae *s.l.*; or dimerous: *Putranjiva formosana* (Kaneh. & Sasaki ex Shimada) Kaneh. (Tokuoka & Peng, 1997) – some Euphorbiaceae *s.s.*, some Phyllanthaceae, e.g. species of *Phyllanthus* L. (Pax & Hoffmann, 1931; Zhang *et al.*, 2012).
3. Multicellular hairs on floral organs: Putranjivaceae – many Euphorbiaceae *s.l.*, especially Euphorbiaceae *s.s.* (Pax & Hoffmann, 1931).
4. Short synsepaly: Lophopyxidaceae, common in Putranjivaceae – many Euphorbiaceae *s.s.*, Peraceae (male flowers of *Pera* Mutis if a calyx is present; Bigio & Secco, 2012), some Phyllanthaceae (Pax & Hoffmann, 1931).
5. Absence of petals: Putranjivaceae – most Euphorbiaceae *s.l.* (Pax & Hoffmann, 1931).
6. Stamens antesepalous (in haplostemonous flowers): Lophopyxidaceae, Putranjivaceae – Euphorbiaceae *s.l.* (see Pax & Hoffmann, 1931).
7. Polystemony: many *Drypetes* spp. – many Euphorbiaceae *s.s.*, some Phyllanthaceae) (Pax & Hoffmann, 1931).
8. Gynoecium with more than five carpels: Putranjivaceae (*D. gossweileri*) – several Euphorbiaceae *s.s.*, some Phyllanthaceae (Pax & Hoffmann, 1931).
9. Gynoecium probably pseudomonomerous: *Sibangea*, *Drypetes* p.p. – a few Euphorbiaceae *s.s.* (*Crotonopsis* Michx., *Eremocarpus* Lindl.; Radcliffe-Smith, 2001).
10. Stigmatic branches bilobed: *Putranjiva*, some *Drypetes* – many Euphorbiaceae *s.s.*, many Phyllanthaceae (e.g. Sutter & Endress, 1995).
11. Stigmatic branches with ventral furrow: Lophopyxidaceae, *Sibangea* of Putranjivaceae – common in Euphorbiaceae *s.l.* (Sutter & Endress, 1995).
12. Placenta axile: Lophopyxidaceae, all Putranjivaceae – all Euphorbiaceae *s.l.* (Pax & Hoffmann, 1931).
13. Two collateral antitropous ovules present per carpel, with obturator: Lophopyxidaceae, all Putranjivaceae – all Euphorbiaceae *s.l.*, except for Euphorbiaceae (*s.s.*), with a single median antitropous ovule with obturator.
14. Placenta located in the upper synascidiate zone, obturators in the uppermost synascidiate and lowermost symplicate zones: Lophopyxidaceae, all Putranjivaceae – all Euphorbiaceae *s.l.* (e.g. Merino Sutter, Forster & Endress, 2006).
15. Inner integuments thicker than outer: Lophopyxidaceae, all Putranjivaceae studied (except *Drypetes gossweileri*, with both integuments equally thick) – most Euphorbiaceae *s.l.* (e.g. Merino Sutter *et al.*, 2006), but also many other Malpighiales and other malvids (Endress & Matthews, 2006).
16. Obturator protruding into micropyle: scarce in Putranjivaceae – various Euphorbiaceae *s.l.* (Sutter & Endress, 1995).
17. Gap between integuments: *Putranjiva*, some *Drypetes* spp.; this study – Euphorbiaceae *s.s.*, Phyllanthaceae (Sutter & Endress, 1995); Picrodendraceae (Merino Sutter *et al.*, 2006).
18. Vascular bundles in integuments: outer integument in *Putranjiva* (this study; Singh, 1970), many *Drypetes* and *Sibangea* (this study) – outer or inner integument in various Euphorbiaceae (Tokuoka & Tobe, 1995, 2002, 2003; Tokuoka, 2007), rarely outer in Phyllanthaceae (Tokuoka & Tobe, 2001), rarely slightly inner in Picrodendraceae (Merino Sutter *et al.*, 2006).
19. Nectary absent: *Putranjiva* – a number of Euphorbiaceae *s.l.* (Pax & Hoffmann, 1931).
20. Wind pollination: *Putranjiva* – some Euphorbiaceae *s.l.* (Webster, 1994a).

## Differences (features of special interest in bold)

1. **Ovules only weakly crassinucellar or incompletely tenuinucellar** (Tokuoka & Tobe, 1999) vs. crassinucellar in Euphorbiaceae *s.l.*
2. **Endothelium present** (Tokuoka & Tobe, 1999) vs. absent in Euphorbiaceae *s.l.*
3. **Nucellus long and slender, without nucellar cap or nucellar beak** vs. thicker and with beak in many Euphorbiaceae *s.l.* (but also in some Euphorbiaceae *s.s.*, such as species of *Hura* L. and *Mallotus* Lour., a nucellar beak is lacking, Rao, 1970; and, in Picrodendraceae, a beak may be present or absent, whereas a cap is commonly present, Merino Sutter *et al.*, 2006).
4. **Micropyle present** vs. absent in Euphorbiaceae *s.l.* with a prominent nucellar beak (Zhang *et al.*, 2012).
5. Fruit indehiscent (dehiscent in most Euphorbiaceae *s.l.*, Pax & Hoffmann, 1931; Radcliffe-Smith, 2001).

*Comparison of Lophopyxidaceae and Putranjivaceae with Malpighiales (other than Euphorbiaceae, Phyllanthaceae, Picrodendraceae and Peraceae)*

A number of features of Lophopyxidaceae and Putranjivaceae are not shared with Euphorbiaceae *s.l.*, but

with other Malpighiales, or are shared with other Malpighiales **plus** Euphorbiaceae *s.l.* (features of special interest at this level in bold).

- 1. Glands on sepal margins:** *Sibangea* – similar in some Linaceae and Ochnaceae (Matthews & Endress, 2011; Matthews *et al.*, 2012).
- 2. Petals present:** *Lophopyxis* – many other Malpighiales.
- 3. Ovules two per carpel and antitropous and mostly with obturator:** *Lophopyxis*, all Putranjivaceae – many other Malpighiales, such as Chrysobalanaceae *s.l.* plus Balanopaceae (Merino Sutter & Endress, 2003; Matthews & Endress, 2008), many Rhizophoraceae plus Ctenolophonaceae (Matthews & Endress, 2011; for Rhizophoraceae, also Tobe & Raven, 1987), Linaceae (Matthews & Endress, 2011), Humiriaceae and Ixonanthaceae (Rao & Narayana, 1965; Narayana & Rao, 1966, 1969; Boesewinkel, 1985), Quiinaceae plus Medusagynaceae (Matthews *et al.*, 2012; for Medusagynaceae, also Dickison, 1990). When an obturator is present, the ovules are pendant.
- 4. Ovules weakly crassinucellar or incompletely tenuinucellar with endothelium and nucellus long and slender:** *Lophopyxis*, most Putranjivaceae – many other Malpighiales; in some Putranjivaceae, the ovules are technically crassinucellar (Thathachar, 1953; Tokuoka & Tobe, 1999), but even these have an endothelium, which is an unusual combination in angiosperms and is also known from some Rhizophoraceae (Matthews & Endress, 2011).
- 5. Ovules without nucellar beak, micropyle present:** *Lophopyxis*, all Putranjivaceae – most Malpighiales.
- 6. Pedicel abscission zone present:** part of Putranjivaceae – many other Malpighiales (Stevens, 2001 onwards; Matthews & Endress, 2008, 2011; Matthews *et al.*, 2012).
- 7. Fruit indehiscent:** *Lophopyxis* and all Putranjivaceae – a number of other Malpighiales.

*Comparison of Lophopyxidaceae and Putranjivaceae with other subclades of clade 3 (sensu Xi *et al.*, 2012)*

In the most recent phylogenetic analysis of Malpighiales, the order forms three major subclades (Xi *et al.*, 2012). Lophopyxidaceae and Putranjivaceae are in subclade 3, together with ‘chrysobalanoids’ (Chrysobalanaceae, Euphroniaceae, Dichapetalaceae, Trigoniaceae, Balanopaceae), ‘malpighioids’ (Malpighiaceae, Elatinaceae, Centroplacaceae) and Caryocaraceae. However, there is no resolution between these components. In the families of clade 3, there is a tendency to the bulging of ovaries (and apical

septum), a slender nucellus and mostly axile placentation (see Fig. 1 in Endress *et al.*, 2013).

## CONCLUSIONS

That Putranjivaceae are not part of Euphorbiaceae *s.l.*, but belong to another branch of the phylogenetic tree of Malpighiales, as shown in molecular phylogenetic studies (Wurdack & Davis, 2009; Soltis *et al.*, 2011; Xi *et al.*, 2012), is clearly supported by the present comparative investigations of floral structure. Superficial similarities between Putranjivaceae and Euphorbiaceae *s.l.*, such as inconspicuous flowers without petals and often trimery, and the partial lack of nectaries, are probably convergent. The sister relationship of Putranjivaceae and Lophopyxidaceae is corroborated by floral structure. A suite of unusual characters related to the ovules is of special interest in these families and other groups of Malpighiales (Endress *et al.*, 2013). These features need to be critically studied and compared throughout the family-rich order Malpighiales.

## ACKNOWLEDGEMENTS

We especially thank K. Seshagirirao and his colleagues, V. S. Raju and L. Harikrishnanaik (UH), for the collection of liquid-fixed *Putranjiva* material. For liquid-fixed and herbarium material, we thank A. Bond and G. Challen (K), G. Theisse (L) and F. Aleva (WAG). For liquid-fixed material, we thank P. Forster and A. Bolin (BRI) and F. Zich (CNS). For herbarium material, we thank P. Stevens (MO), P. Venu (BSID) and N. S. Atri (PUN). There were also a great many people who assisted M.L.M. in her search for flowering material of Putranjivaceae, including J. Schönenberger and R. Samuel (University of Vienna), L. Ronse De Craene (University of Edinburgh) and E. Smets (L). D. Dixon (NSW) is thanked for help in searching for Australian *Drypetes* material and M. do C. E. Amaral (UNICAMP) for Brazilian *Drypetes* material. Peter Linder (Z), M. Cheek (K), T. McFarlane (BOL), Q. Blake, P. Bruyns and L. Newton are thanked for their help in searching for African Putranjivaceae material. For *Putranjiva* material, M.L.M. received offers of help or advice from many people, including D. Yakandawala (University of Peradeniya, Sri Lanka) and, in India, from P. S. S. V. Khan (Yogi Verma University), S. Yadav (SUK), T. Husain (LWG), G. C. Sarma (GUBH), Y. S. Bedi (Plant Biotechnology Division, Jammu), A. K. Goel (CSIR-NBRI), A. A. Mao (ARUN), A. K. Pandey (University of Delhi), D. Shah (BARO), M. N. Srivastava (Central Drug Research Institute, Lucknow), G. Satheesh (CMPR),

M. Sabu (University of Calicut) and P. B. Singh (JHS). Reto Nyffeler (Z) is especially thanked for assistance in contacting all Indian herbaria in search of material of *Putranjiva*. Anita Lendel is thanked for most of the microtome sections and the Centre for Microscopy and Microanalysis (ZMB), University of Zurich is thanked for assistance with SEM. This study is part of the project 'Flower diversity and evolution in rosids' of P.K.E., supported by grant # 31003A\_129804 of the Swiss National Foundation (SNF) and the Institute of Systematic Botany, University of Zurich, Switzerland. We are indebted to Michael Fay and two anonymous reviewers for their comments on the manuscript.

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