

Elaborate petals and staminodes in eudicots: Diversity, function, and evolution

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Dedicated to Stefan Vogel, Vienna, on the occasion of his 80th birthday

Abstract

Petals, a characteristic feature of eudicots, have evolved elaborations in various ways and across diverse clades. In this survey of petal and staminode elaborations throughout the eudicots, based on both new studies and a review of the literature, the diversity of such structures and their functions is discussed. Petal elaborations are primarily present as marginal lobes and ventral lobes of various shapes. Lobation patterns can be loosely classified as pinnate, binate, or ternate. One of these patterns may be dominant within a family (e.g. pinnate in Anisophylleaceae, binate in Caryophyllaceae, ternate in Elaeocarpaceae); transitional forms also occur (e.g. between binate and ternate in Onagraceae). Coronas between the corolla and androecium are found in several groups, for example in several families of Malpighiales or in Apocynaceae. In some clades, petal elaborations are especially prominent and can be used as approximate systematic markers (Anisophylleaceae, Elaeocarpaceae, Rhizophoraceae). Petal elaborations are especially diverse in rosids. In asterids, which are characterized by sympetaly, elaborations are more conspicuous at the level of the architecture of the entire corolla, rather than at the level of individual petals. Evolutionary trends in petal elaboration in certain larger clades are shown and their involvement in floral biological functions is discussed. © 2006 Gesellschaft für Biologische Systematik. Published by Elsevier GmbH. All rights reserved.

Keywords: Eudicots; Petals; Corona; Staminodes; Flower diversity; Flower evolution

Introduction

Petals in general form the second series or whorl of floral organs and are the main optically attractive organs of flowers. Although conspicuous, they are commonly the most structurally simple organs, if morphology and histology are considered together. The presence of petals is a typical feature of eudicots, and it remains uncertain to what extent the petal-like organs in other angiosperms are homologous to the

petals of eudicots. In addition to simple petal forms, in some eudicots, subdivided and otherwise elaborate petal forms have evolved. Such elaborate petals develop with a diversity of patterns and apparently have acquired diverse functions in different plant groups. However, their structure, function and diversity are poorly explored. Such elaborate petals may have marginal or ventral lobes or an elaborate tip. Dorsal or ventral invaginations produce hollow scales or spurs. Localized hair pads may play a role in the total floral architecture. We especially concentrate on lobed organs. Lobed petals are also known from Eocene and Oligocene (cunoniaceous) fossils (Carpenter and Buchanan 1993).

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Staminodes may also be elaborate, and since there appears to be a structural and evolutionary affinity of petals to stamens (staminodes), it is useful to include the latter in a comparative study of elaborate petals.

Petal diversity has found attention especially at the level of epidermis differentiation, which greatly affects optical (and perhaps also tactile) properties (Ehler 1975; Kay et al. 1981; Christensen and Hansen 1998). But comparative morphological and functional aspects other than surface differentiation have not been studied at a larger scale since the accounts by Glück (1919; vascular patterns), von Gumpenberg (1924; developmental patterns), and Troll (1928; petal shape). The developmental and evolutionary relationship between petals, sepals and stamens is now being addressed by the field of evo-devo (Albert et al. 1998; Baum and Whitlock 1999; Kramer and Irish 1999, 2000; Irish 2003; Kramer et al. 2003; Soltis et al. 2004). Recently, the diversity of petals and its systematic significance was addressed in some orders of rosids (Matthews and Endress 2002, 2004, 2005a, b).

Another aspect, the diversity and systematic distribution of petal (and staminode) elaborations across the eudicots, is the topic of the present study. Such a comparative study seems timely, since we have assembled a representative sample of wet-preserved collections for most of the families with the most elaborate petal and staminode forms. The study combines original results with a review. We do not focus on sympetaly or on fusion of petals and stamens, which are important innovations in asterids and a few smaller clades of eudicots. We also do not focus on developmental aspects. This dimension would need much additional study. For the systematic framework we generally follow the classification proposed in APG (2003).

Three topics are addressed in this comparative study in particular: (1) basic patterns among the diversity of elaborate petals and staminodes, and homology of problematic cases; (2) potential functions of the elaborate structures; (3) systematic and evolutionary aspects of the elaborate structures. Thus, this study should also provide a basis for future developmental/genetic and evolutionary studies.

Material and methods

The taxa studied are listed in Table 1. Flowers were fixed in FAA or 70% ethanol and examined with the SEM after critical-point drying and sputter-coating with gold. For some species microtome serial sections were produced, either from paraplast-embedded material, stained with safranin and astra blue, or from methacrylate-embedded material, stained with ruthenium red and toluidine blue, and mounted in Histomount.

In the figures, SEM micrographs are from authentic flowers unless otherwise specified.

Results

We follow the classification of APG (2003). Larger clades in which no elaborate petals occur are not mentioned in the section “Results”.

Basal eudicots

The most complicated petals among basal eudicots are found in Ranunculales. In ‘core’ Ranunculales (including Ranunculaceae, Berberidaceae, Menispermaceae, Lardizabalaceae), this complication is associated with the presence of nectaries on the petals. However, in Papaveraceae, which appear as sister to all other Ranunculales (Hoot and Crane 1995; Soltis et al. 2000), petals do not have nectaries. In Ranunculaceae and Berberidaceae the nectaries are often located in grooves or spurs (Tamura 1995). Mostly there is one groove at the ventral base of the petal; rarely several grooves are arranged in an arc (*Ranunculus crithmifolius*; Fisher 1965; *Laccopetalum*; Hiepko 1965). The grooves may be simple concavities or covered by a lid (e.g. *Ranunculus*, *Nigella*) (Figs. 1A–D, 13G). In *Nigella*, two glistening convexities, which probably act as pseudonectaries, are also present on the petals (Fig. 1C). Pseudonectaries at the petal tips are also present in certain species of *Eranthis* and *Trollius*. Petals are tubular, with the nectary at the base of the tube (e.g. *Helleborus*), and they have spurs in *Aquilegia*, *Aconitum*, and *Delphinium* (e.g. Hiepko 1965; Kosuge and Tamura 1988; Kosuge 1994; Hodges 1997; Erbar et al. 1998). Among Berberidaceae, petals with spurs are present in *Epimedium* and *Vancouveria* (e.g. Hiepko 1965). In Menispermaceae, Lardizabalaceae, and other Berberidaceae, if petals have nectaries they are not immersed in grooves or spurs (e.g. Smets 1986; Endress 1995). Elaborations that are not connected with nectaries or pseudonectaries are rare in Ranunculaceae. However, the petals may be bilobed (*Cimicifuga*, *Delphinium*, *Nigella*) or irregularly lobulate or denticulate in, e.g., *Helleborus* and *Souliea* (Tamura 1995).

In Papaveraceae–Fumarioideae, in *Hypecoum* the petals are trilobed, and on the two inner petals the middle lobe is crenulate and papillate and functions in secondary pollen presentation (Dahl 1989; Yeo 1993) (Fig. 1E, F). In other Fumarioideae with more elaborate flowers, the inner two petals are postgenitally fused at the tip of the middle lobe (the side lobes being shorter) and form a container for the pollination organs, like a keel that works in two directions; in addition, they are congenitally fused to various degrees with the outer

Table 1. Fixed material studied (E = collections by P.K. Endress)

Family	Species	Collection details
Achariaceae	<i>Ryparosa javanica</i> Koord. et Valetton	E 4225, northern Queensland, Australia
Anisophylleaceae	<i>Anisophyllea disticha</i> Baill.	A.M. Juncosa s.n., X 81, Brunei
	<i>Combretocarpus rotundatus</i> Dans.	A.M. Juncosa s.n., 27 X 81 A, Brunei
	<i>Polygonanthus amazonicus</i> Ducke	A.M. Juncosa, s.n., s.d., Brazil
Argophyllaceae	<i>Argophyllum cryptophlebium</i> Zemann	E 9233, northern Queensland, Australia
	<i>Corokia cotoneaster</i> Raoul	E 7356, cult. Bot. Garden, Univ. of Zurich, Switzerland
Bruniaceae	<i>Berzelia lanuginosa</i> Brongn.	H.U. Stauffer 5039, South Africa
Caryophyllaceae	<i>Silene multifida</i> Edgew.	E 00-57, cult. Bot. Garden, Univ. of Zurich, Switzerland
Celastraceae	<i>Brexia madagascariensis</i> Thouars	E 6779, cult. Bot. Garden Hamburg, Germany
	<i>Salacighia letestuana</i> Blakelock	E 97-29, Ivory Coast
Corynocarpaceae	<i>Corynocarpus laevigata</i> Forst.	E 6369, New Zealand
Cucurbitaceae	<i>Trichosanthes cucumerina</i> L.	M.L. Matthews 066, cult. Bot. Garden, Univ. of Zurich, Switzerland
Cunoniaceae	<i>Ceratopetalum gummiferum</i> Sm.	E 5093, E 6162, E 6344, cult. old Bot. Garden Brisbane, Australia
	<i>Gillbeea adenopetala</i> F. Muell.	E 4273, E 9073, northern Queensland, Australia
	<i>Schizomeria whitei</i> Mattf.	E 4209, northern Queensland, Australia
Elaeocarpaceae	<i>Aristotelia serrata</i> W.R.B. Oliv.	E 6381, New Zealand
	<i>Crinodendron hookerianum</i> Gay	E 7431, E 7699, cult. Bot. Garden, Univ. of Zurich, Switzerland
	<i>Crinodendron patagua</i> Molina	E 2649, cult. old Bot. Garden, Univ. of Zurich, Switzerland
	<i>Elaeocarpus reticulatus</i> Sm.	M.L. Matthews 019, Victoria, Australia
	<i>Elaeocarpus</i> cf. <i>subvillosus</i> Arn.	E 00-14a, cult. Fazenda St. Eliza, Campinas, S.P., Brazil
Erythroxylaceae	<i>Erythroxylum novogranatense</i> (Morris) Hieron.	E 952, cult. old Bot. Garden, Univ. of Zurich, Switzerland
Euphorbiaceae	<i>Clutia</i> spec.	E 02-63, South Africa
Frankeniaceae	<i>Frankenia thymifolia</i> Desf.	E s.n., coll. 02.05.1971, Algeria
Loasaceae	<i>Blumenbachia hieronymi</i> Urb.	E 6658, cult. Bot. Garden, Univ. of Zurich, Switzerland
	<i>Nasa triphylla</i> (Juss.) Weigend	E 4827, cult. Bot. Garden, Univ. of Zurich, Switzerland
Loganiaceae	<i>Neuburgia celebica</i> (Koord.) Leenh.	E 03-22, cult. National Tropical Bot. Garden, Kauai, Hawaii, USA
Malvaceae	<i>Commersonia fraseri</i> J. Gay	E 03-54, cult. National Tropical Bot. Garden, Kauai, Hawaii, USA
	<i>Grewia crenata</i> Mast.	E 03-70, cult. National Tropical Bot. Garden, Kauai, Hawaii, USA
Melanthaceae	<i>Greyia sutherlandii</i> Hook. et Harv.	U. Hofmann s.n., s.d., cult. Bot. Garden, Univ. of Göttingen, Germany
Olacaceae	<i>Schoepfia chrysophylloides</i> (A. Rich.) Planch.	E 02-24, Florida, USA
Oxalidaceae	<i>Averrhoa carambola</i> L.	E 4158, cult. Bot. Garden Lae, Papua New Guinea
Papaveraceae	<i>Hypocoum procumbens</i> L.	E 00-48, cult. Bot. Garden, Univ. of Zurich, Switzerland
Parnassiaceae	<i>Parnassia fimbriata</i> Banks	E 7483, Washington State, USA
	<i>Parnassia palustris</i> L.	E 5228, E 5237, Switzerland
Polygalaceae	<i>Muraltia</i> spec.	E 02-59, South Africa
	<i>Nylandtia</i> spec.	E 02-77, South Africa
	<i>Polygala vulgaris</i> L.	E 5148, Switzerland
Ranunculaceae	<i>Nigella arvensis</i> L.	E 9894, cult. Bot. Garden, Univ. of Zurich, Switzerland
	<i>Nigella garidella</i> Spenn.	E 97-53, cult. Bot. Garden, Univ. of Zurich, Switzerland
Resedaceae	<i>Reseda luteola</i> L.	E 7645, cult. Bot. Garden, Univ. of Zurich, Switzerland
Rhizophoraceae	<i>Bruguiera cylindrica</i> (L.) Bl.	A.M. Juncosa s.n., s.d.
	<i>Bruguiera gymnorrhiza</i> (L.) Lamk.	E 9834, cult. Bot. Garden, Univ. of Zurich, Switzerland
	<i>Carallia borneensis</i> Oliv.	A.M. Juncosa s.n., X 81, Brunei
	<i>Cassipourea</i> spec.	A.M. Juncosa s.n., s.d., Monteverde, Costa Rica
	<i>Ceriops decandra</i> (Griff.) Ding Hou	E 9206, northern Queensland, Australia
	<i>Ceriops tagal</i> (Perr.) C. Robinson	E 9205, northern Queensland, Australia
	<i>Crossostylis grandiflora</i> Brongn. & Gris	A.M. Juncosa s.n., s.d., New Caledonia
	<i>Gynotroches axillaris</i> Bl.	A.M. Juncosa s.n., 9 X 81, Sarawak

Table 1. (continued)

Family	Species	Collection details
	<i>Pellacalyx cristatus</i> Hemsl.	A.M. Juncosa s.n., 10 X 81, Sarawak
	<i>Rhizophora x lamarekii</i> Montr.	E 6209, New Caledonia
	<i>Rhizophora</i> cf. <i>mucronata</i> Lamk.	E 9204, northern Queensland, Australia
	<i>Rhizophora stylosa</i> Griff.	A.M. Juncosa s.n., s.d., New Caledonia
Santalaceae	<i>Thesium</i> spec.	E 02-53, South Africa
Sapindaceae	<i>Cardiospermum halicacabum</i> L.	E 6730, cult. Bot. Garden, Univ. of Zurich, Switzerland
Sapotaceae	<i>Mimusops commersonii</i> Engl.	E 03-19, cult. National Tropical Bot. Garden, Kauai, Hawaii, USA
Saxifragaceae	<i>Mitella pentandra</i> Hook.	E 9830, cult. Bot. Garden, Univ. of Zurich, Switzerland
	<i>Tellima grandiflora</i> (Pursh) Dougl.	E 9828, cult. Bot. Garden, Univ. of Zurich, Switzerland
Tropaeolaceae	<i>Tropaeolum peregrinum</i> L.	E 8007, cult. Bot. Garden, Univ. of Zurich, Switzerland

petal pair. In *Corydalis* and *Dicentra* and their relatives, one or two of the outer petals form conspicuous spurs and may function as nectar holders. However, the nectaries themselves are located at the base of the stamen and not on the petals. In *Corydalis*, the nectaries may be secondarily displaced for some distance into the spur by the intercalary elongation of the spur. In the other subfamilies of Papaveraceae with open, bowl-shaped flowers the petals are not elaborate. Lacinate petals are known from horticultural mutants of simple wild forms, e.g. in *Chelidonium majus* and *Papaver somniferum*.

In most other clades of basal eudicots petals are lacking (Proteaceae, Buxaceae, Trochodendraceae) (Endress 1986; Douglas and Tucker 1996; von Balthazar and Endress 2002a, b), or their presence is doubtful (*Nelumbo*, *Platanus*; Hiepko 1965), although Haynes et al. (2000) describe the colored perianth organs as petals. Only in Sabiaceae do petals appear to be present; where they are bilobed and sometimes additionally fringed, they also appear to have ventral appendages (van Beusekom 1971). However, the morphological interpretation of these structures is unclear, and developmental studies would be helpful for this problem.

Core eudicots – Dilleniaceae

In some species of *Hibbertia* the petals are bilobed. *Pachynema sphenandrum* has a corona consisting of an irregularly lobed, membranous sheath (potentially derived from staminodes), which surrounds the stamens (Craven and Dunlop 1992).

Core eudicots – Caryophyllales

A number of families of Caryophyllales do not have petals, and conspicuously elaborate petals are not

common, except in Caryophyllaceae. Many Caryophyllaceae have emarginate or two-lobed petals. In addition, a common feature in a number of Caryophylloideae (Bittrich 1993) are two ventral lobes (corona) on the petals or two longitudinal ridges along the claw (Fig. 13I) (e.g. Rohweder 1967; Pirker and Greuter 1997). *Dianthus* commonly has dentate petal blades at the periphery of the corolla. In some species of *Dianthus* (*D. superbus*, *D. monspessulanus*; Glück 1919) and several species of *Silene* (*S. multifida*, *S. polypetala*, *S. gangotriana*; for the latter see Pusalkar et al. 2004) the petals are subdivided into numerous long lobes (Fig. 2A). A pattern shared among these simple and complicated forms of lobed petals in Caryophylloideae is that a middle lobe is lacking (Fig. 13B) (not obvious in *Dianthus*). Thus, the excessively divided patterns originate by repeated bifurcation of the two primary lateral lobes. The same pattern of repeated bifurcation is also present in several species of *Drymaria* (Paronychioideae) (Duke 1961), and in several genera of Alsinoideae, such as *Arenaria* (e.g. *A. pogonantha*, *A. auricoma*) (Zhou and Wu 1996), *Cerastium* (*C. schizopetalum*) (Kitamura and Murata 1961), and *Stellaria* (*S. radians*) (Wu and Ke 1996). Apparently, this pattern evolved separately in the different groups, and thus may have arisen many times within the family. An exception to the general bilobed (or multiply bilobed) pattern that is so common in Caryophyllaceae is found in a few species of Paronychioideae, in which three-lobed petals occur with one central and two lateral lobes. This form is present in species of *Cardionema* (as *Acanthonychia*) (Rohrbach 1872), and in *Achyronychia* and *Pollichia* (Kraft 1917; Rohweder 1970). However, in general in Paronychioideae the petals are small and linear or lacking (Rohweder 1970; Bittrich 1993).

In some Amaranthaceae s.str. interstaminal, often lacinate, appendages are present (e.g. *Achyranthes*, *Alternanthera*). They have been referred to as pseudo-staminodia (Eliasson 1988) but their nature is uncertain.

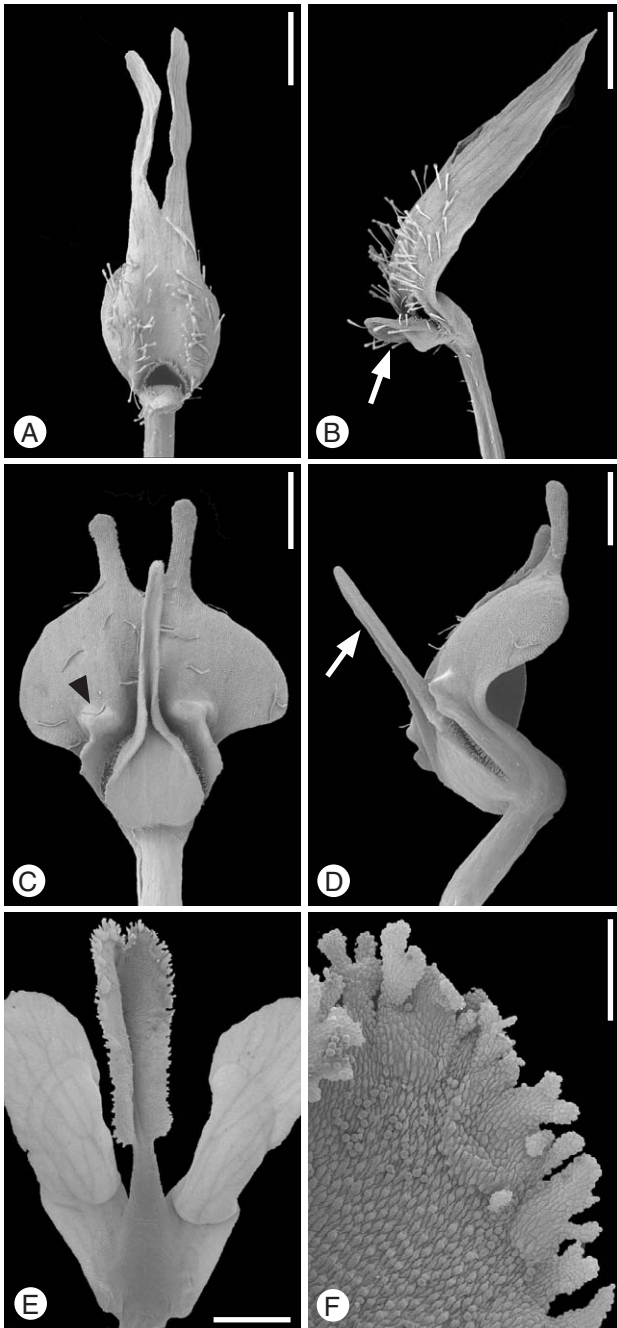


Fig. 1. Ranunculales. (A, B) *Nigella garidella* (Ranunculaceae), petal; (A) from ventral; (B) from the side (arrow: ventral lobe). (C, D) *Nigella arvensis* (Ranunculaceae), petal; (C) from ventral (arrowhead: pseudonectary); (D) from the side (arrow: ventral lobe). (E, F) *Hypocoum procumbens* (Papaveraceae), inner petal; (E) from ventral; (F) mid-lobe, from ventral. Scale bars: A–E = 1 mm; F = 0.2 mm.

In almost all Frankeniaceae, petals have a ventral scale, which may be differentiated as a ligule or as two sublateral wings (Glück 1919; Leinfellner 1965) (Fig. 2B). *Reaumuria* (Tamaricaceae) has petals with

two lateral fringed scales near their ventral base (Ronse De Craene 1990; Gaskin 2002).

Core eudicots – Santalales

In families of Santalales with two perianth whorls, the inner whorl (corolla) is always larger and protective; in families with only one perianth whorl, this whorl also likely corresponds to a corolla (Endress 1994). The petals in many species of *Thesium* (Santalaceae) are adorned with numerous multicellular outgrowths on the ventral side (Fig. 2C–E). The presence of dense tufts of hairs on the inner side of the petals is also known from other Santalaceae; but their detailed structure is unknown (e.g. *Exocarpos*; Stauffer 1959; *Okoubaka*; Hallé 1987). Also, in Olacaceae there tend to be dense carpets of hairs on the inner petal surface. In *Schoepfia*, these hairs are uniseriate and moniliform (Fig. 2F, G). In other taxa their detailed structure is unknown (e.g. *Heisteria*; Klein 1988; *Phanerodiscus*; Malécot et al. 2003). In both families the hairs occur either as tufts in a position just above the anthers in bud (*Okoubaka*, *Heisteria*, *Schoepfia*), or they appear as a carpet on the entire inner surface of the petal (*Exocarpos*, *Phanerodiscus*, *Ximenia*). Elaborations other than hairs on the petals have not been found in Santalales.

Core eudicots – Saxifragales

In Saxifragales, variation between presence and absence of petals is quite common, even within families or genera. Rarely, lobed petals are present. The small families Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, and Penthoraceae do not have petals at all. In Haloragaceae petals are present or absent (Orchard 1975), with both conditions occurring even within genera: in *Aphanopetalum* (included in Haloragaceae by Soltis et al. 2005) one of the two included species has (small, linear) petals, the other lacks petals. In Hamamelidaceae, where petals are present they are mostly strap-shaped and circinate in bud, but they are absent in many genera, short and filamentous in *Fortunearia*, and tiny or absent in *Sinowilsonia* (Endress 1989a, b); the strap-shaped petals have two basal lateral lobes in *Embolanthera* (Endress 1989b).

In Saxifragaceae, petals are present or absent, this lability being evident also at tribe, or genus level (*Astilbe*, *Rodgersia*, *Saxifraga*, *Tiarella*, *Heuchera*) (Engler 1930a). In the four genera *Lithophragma*, *Mitella*, *Tellima* and *Tiarella* divided petals are present, especially in *Mitella* and *Tellima* with very narrow lobes. These genera are all part of the “*Heuchera* group”, a small clade within the family (Johnson and Soltis 1994; Soltis et al. 2001). Also, *Tolmiea* with filamentous but undivided petals belongs with this group. The divided

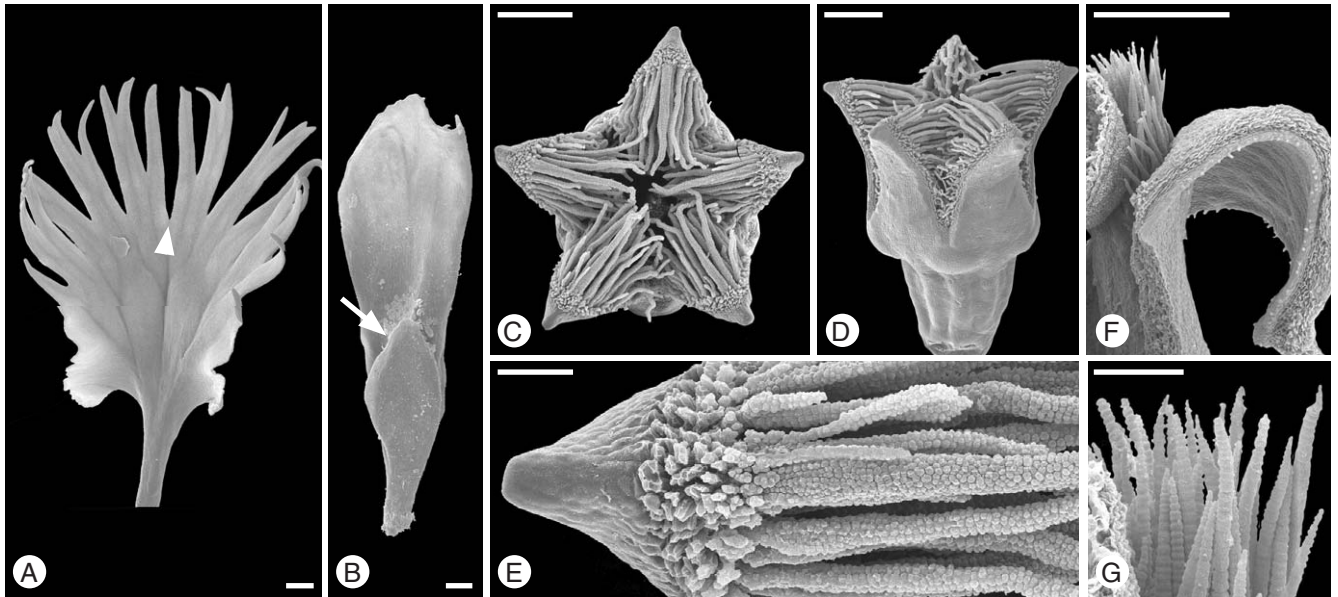


Fig. 2. Caryophyllales and Santalales. (A) *Silene multifida* (Caryophyllaceae), petal, from ventral (arrowhead: deepest incision). (B) *Frankenia thymifolia* (Frankeniaceae), petal, from ventral (arrow: ventral lobe). (C–E) *Thesium* spec. (Santalaceae); (C) flower, from above; (D) flower, from the side; (E) petal, from ventral. (F, G) *Schoepfia chrysophylloides* (Olacaceae); (F) petal with tuft of hairs (and part of anther), from the side; (G) tuft of petal hairs, magnified. Scale bars: A, C, D, F = 0.5 mm; B, E, G = 0.1 mm.

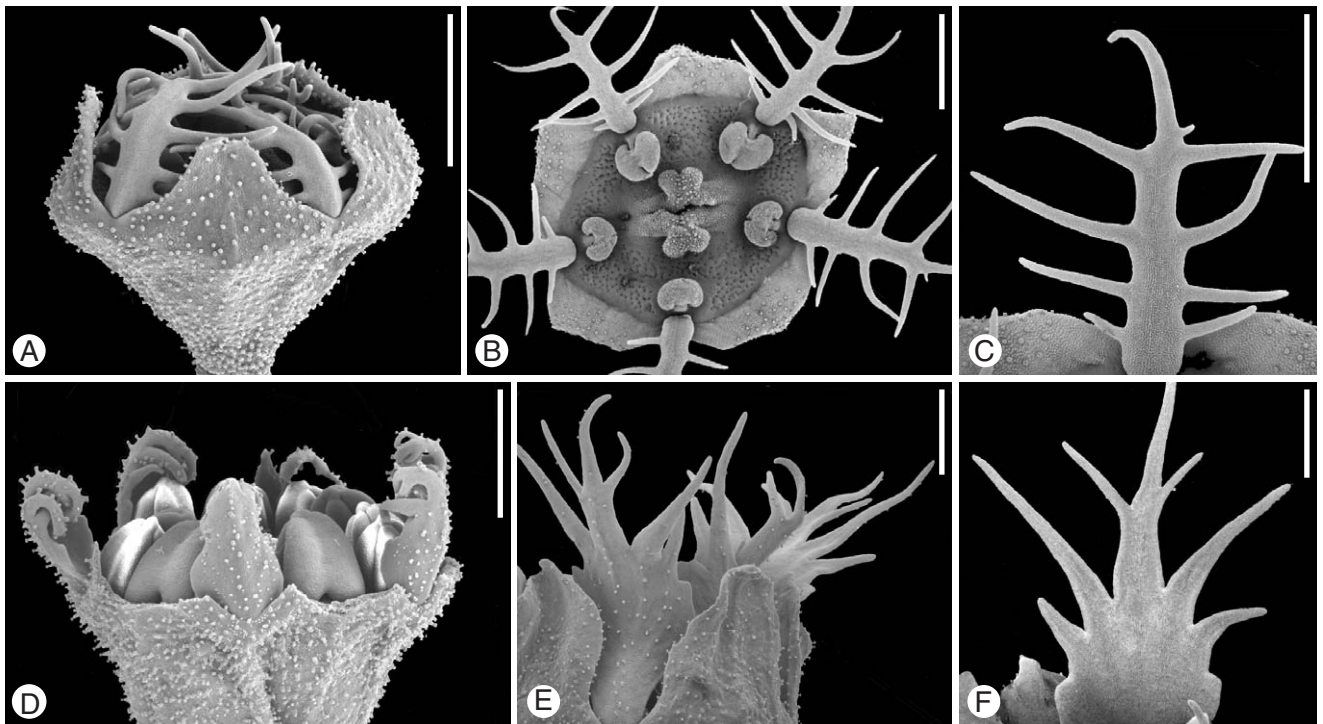


Fig. 3. Saxifragaceae. (A–C) *Mitella pentandra*; (A) opening flower, from the side; (B) flower, from above; (C) petal, from ventral. (D–F) *Tellima grandiflora*; (D) opening flower, from the side; (E) flower, from the side; (F) petal, from ventral. Scale bars = 1 mm.

petals of the *Heuchera* group always have a median lobe. They are flat and spreading at anthesis. *Mitella* and *Tellima* have pinnatifid petals, sometimes with more

than ten lobes (Fig. 3). In bud, the petals of the species studied here are connivent over the stamens; in *Mitella* the petal lobes themselves are straight, while in *Tellima*

they are involute (Fig. 3A, D). *Lithophragma* petals are divided or entire; if divided, they are mostly 3–5 lobed, sometimes with additional smaller teeth (Taylor 1965). *Tiarella* petals are three-lobed or entire (Engler 1930a). In *Mitella* the filamentous parts of the pinnate petals have been shown to be holding devices for fungus gnats (Okuyama et al. 2004). This is also true for the simple filamentous petals of *Tolmiea* (Goldblatt et al. 2004). Three-lobed petals were also reported for *Saxifraga cortusifolia* (Nelson 1954), and petals with two small ventral lobes for *Saxifraga hirculus* (Engler 1930a).

Among Crassulaceae, the petals in *Pachyphytum* have a ventral lobe (and are fused with the stamen of the same radius) (Leinfellner 1954c). In *Sedum spectabile* the nectary scale (which potentially corresponds to a staminode) is crenulate (Ronse De Craene and Smets 2001).

In *Pterostemon* (Pterostemonaceae) the staminodes have two lateral teeth (Engler 1930a).

Rosids – Geraniales

Petals are generally present in Geraniales, perhaps with the exception of *Rhynchotheca* (Vivianiaceae) (Weigend 2005). In Geraniaceae, the petals of *Monsonia*, sect. *Odontopetalum* are toothed (Knuth 1931). A few species of *Pelargonium* have laciniate petals, such as *P. amalybicum* (Vogel 1954) and *P. schizopetalum* (van der Walt 1977), or petals with an oblique ventral lobe at the base (*P. adriaanii*; Becker and Albers 2005). Many species of *Geranium* have bilobed petals. The salverform flowers of *G. robertianum* have petals with claws that have two parallel longitudinal ridges on the ventral side (Fig. 13I). The flowers of *Greyia* (Melianthaceae) have ten stalked and peltate (*G. sutherlandii*) or subdivided (*G. flanaganii*) organs, which function as nectaries (Vogel 1954) (Figs. 4A, B, 13F), the nature of which (staminodes or non-staminodes?) is disputed (Ronse De Craene and Smets 1999).

Rosids – Myrtales

In Myrtaceae petals are present (commonly simple) or absent. However, *Verticordia* (“feather flower”) is unusual because of its multiply divided sepals. In most species the petals are also lobed, fringed or toothed, rarely they have, in addition, basal lobes (auricles); also staminodes may be lobed or fringed (Holm 1988; Ye 1993; George 2002). In *Angophora* and relatives the petal tips are differentiated into a ventral (inside the bud) and a dorsal lobe (outside the bud) (Drinnan and Ladiges 1988).

Among Lythraceae, in *Rotala* some species are apetalous, in *R. fimbriata* petals are fimbriate, in some other species slightly lobulate, and in *R. verticillaris* bilobed (Cook 1979). Petals of *Cuphea emarginata* are irregularly bilobed (Koehne 1903). Petals are lobulate in some species of *Lafloensia* and *Lagerstroemia* (Koehne 1903). Fringed disk lobes (staminodes?) are present in *Trapa* (Kadono and Schneider 1986).

Many Onagraceae have bilobed petals. Some *Clarkia* species have petals with three large lobes (e.g. Ford and Gottlieb 1992), *C. biloba* has two lobes, and *C. xantiana* is intermediate with two larger lobes and a tiny midlobe. *Epilobium* also sometimes has deeply bilobed petals (Raven and Raven 1976). In two species of *Lopezia* the petals are laciniate, in others auriculate (Plitmann et al. 1973). Both species with laciniate petals are in the same section *Pelozia*, which is supported as a clade (O’Kane and Schaal 1998) but also contains non-laciniate species. In *Fuchsia* petals are present or absent.

In a clade of Western Gondwanan families of Myrtales (CAROP clade; Clausen and Renner 2001) the petals are relatively small or lacking; they are somewhat lobed (but small) in Rynchocalycaaceae (Schönenberger and Conti 2003).

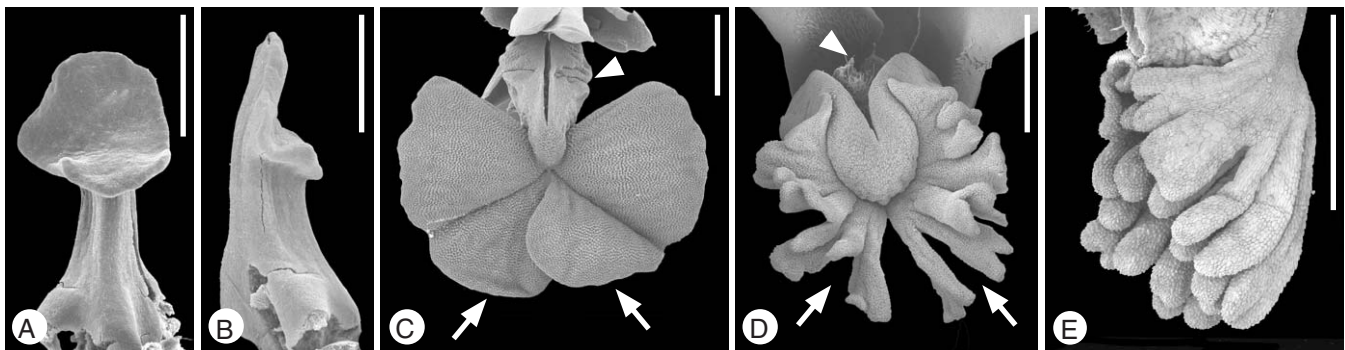


Fig. 4. Geraniales and Fabales. (A, B) *Greyia sutherlandii* (Melianthaceae), staminode-like organ; (A) from ventral; (B) from the side. (C) *Muraltia* spec. (Polygalaceae), keel appendage, from ventral (arrows: two lobes of appendage; arrowhead: keel). (D) *Nylandtia* spec. (Polygalaceae), keel appendage, from ventral (arrows: two lobes of appendage; arrowhead: keel). (E) *Polygala vulgaris* (Polygalaceae), keel appendage, from the side. Scale bars = 1 mm.

Rosids – eurosids I – Zygophyllaceae

In Zygophyllaceae, only the petals of *Augea* (a relative of *Zygophyllum*) are trilobed (Engler 1931).

Rosids – eurosids I – Fabales

All four families of Fabales are characterized by petals but only in the two families with the most complicated flowers do elaborate petals occur.

The monosymmetric flowers of Polygalaceae have a keel formed by the abaxial median petal. In representatives of at least four genera (*Muraltia*, *Nylandtia*, *Polygala*, and *Securidaca*) the distal part of this keel petal has a dorsal appendage that may be simply to multiply lobed (without a median lobe) (Chodat 1897; Heubl 1984; Yeo 1993) (Fig. 4C, D). In *Polygala vulgaris*, for example, there may be more than ten lobes on each side (Fig. 4E). In *Muraltia* this appendage is even larger than the remaining part of the keel (Fig. 4C).

In Fabaceae–Faboideae the complicated architecture of the keel flowers involves elaborate petals. Wing petals commonly have a hook, and each keel petal has a lateral tooth; in some genera the flag petal has a ventral protrusion (e.g. *Lablab*) (Endress 1994). These petal elaborations produce a firm floral architecture. The flag petal is also sometimes bilobed.

Rosids – eurosids I – Rosales

Most families of Rosales do not have petals, and in those that do the petals are mostly not elaborate apart from occasional marginal bilobation. In Rhamnaceae they are generally small and narrow; they may be bilobed or linear (Bennek 1958). In Rosaceae they are present or absent. Some Rosaceae have bilobed petals (e.g. species of *Geum*, *Potentilla*, *Rosa*). *Waldsteinia* has petals with a ventral scale at the base, similar to some Ranunculaceae; however, apparently they do not contain a nectary (Baum 1950; Leinfellner 1954b; Jäger 1961). In *Dirachma* (Dirachmaceae) each petal has a nectary at its ventral base, which is covered by a scale (Link 1991 1994; Ronse De Craene and Miller 2004).

Rosids – eurosids I – Cucurbitales

Anisophylleaceae include three genera (*Anisophyllea*, *Combretocarpus* and *Poga*) with divided petals, while the fourth, *Polygonanthus*, has entire petals with fringed margins (Tobe and Raven 1988; Juncosa and Tomlinson 1989a, b; Matthews et al. 2001; Matthews and Endress 2004). Usually, there are a median and one to several lateral divisions (up to nine in some *Anisophyllea* species; Tobe and Raven 1988). Among the taxa studied,

the petals of *A. disticha* have five divisions, without thickened ends; they cover the stamens in bud and are spreading at anthesis (Fig. 5A, B) (for other *Anisophyllea* species see Ding Hou 1958; Pires and Rodrigues 1971; Floret 1986). The petals of *Combretocarpus* are much shorter than the stamens. They show various stages of reduction from trilobed to bilobed (with one lateral lobe missing) to simple organs (Fig. 5E–G). They may also be extremely small and filamentous, or lacking altogether. Different reduction stages may be found in a single flower. In flowers of *Polygonanthus* the fringed petals are longer than the stamens in bud and cover the anthers (Fig. 5C, D). In some species of *Anisophyllea* and in *Poga*, the petal divisions have thickened apices, which are referred to as glands (Tobe and Raven 1988). There are, however, no studies on the glandular activity of these parts. From the observations by Tobe and Raven (1988) they are full of tracheoids. Based on molecular studies, Anisophylleaceae are in Cucurbitales (Schwarzbach and Ricklefs 2000) and appear as sister to the remaining families of the order (Zhang et al. 2006).

In Corynocarpaceae, in *Corynocarpus laevigata*, the petals are irregularly fringed (Fig. 5H). In addition, there are smaller fringed organs, apparently staminodes, alternating with the petals and bearing a nectary at the ventral base (Philipson 1987; Matthews and Endress 2004) (Fig. 5I, J).

In Cucurbitaceae, in a few genera the petals are deeply bilobed (e.g. *Ceratosanthes*, *Sicyosperma*) (Müller and Pax 1894). In *Hodgsonia*, *Telfairia*, and *Trichosanthes* the petals have long fringes (Fig. 5K, L). The lobes and fringes are commonly involute in bud. In some genera there is a ventral scale on the petals; in *Momordica* and *Thladiantha*, with especially elaborate flowers, this applies to some but not all petals of a flower (Müller and Pax 1894; Zimmermann 1922; Vogel 1990). The genera with fringed petals are more or less highly nested in the family (S.S. Renner, pers. comm.).

In the other families of Cucurbitales petals are mainly lacking (except for Coriariaceae, part of Tetramelaceae, and perhaps some problematical species of *Begonia*) (Matthews and Endress 2004). In Coriariaceae the petals are elaborate histologically but not morphologically, in that they become fleshy and form the outer, attractive part of the drupe-like fruits.

Rosids – eurosids I – Celastrales

Several Celastraceae have fringed petals. They appear scattered in all three larger subfamilies, which appear to form clades (Simmons et al. 2001; Simmons 2004a): Celastroideae (e.g. *Euonymus similis*; Gardner et al. 2000), Hippocrateoideae (*Helictonema*; Hallé 1990; Robson et al. 1994), and Salacioideae (*Salacighia*; Hallé 1990) (Fig. 6A, B). The nectariferous disk may be lobed

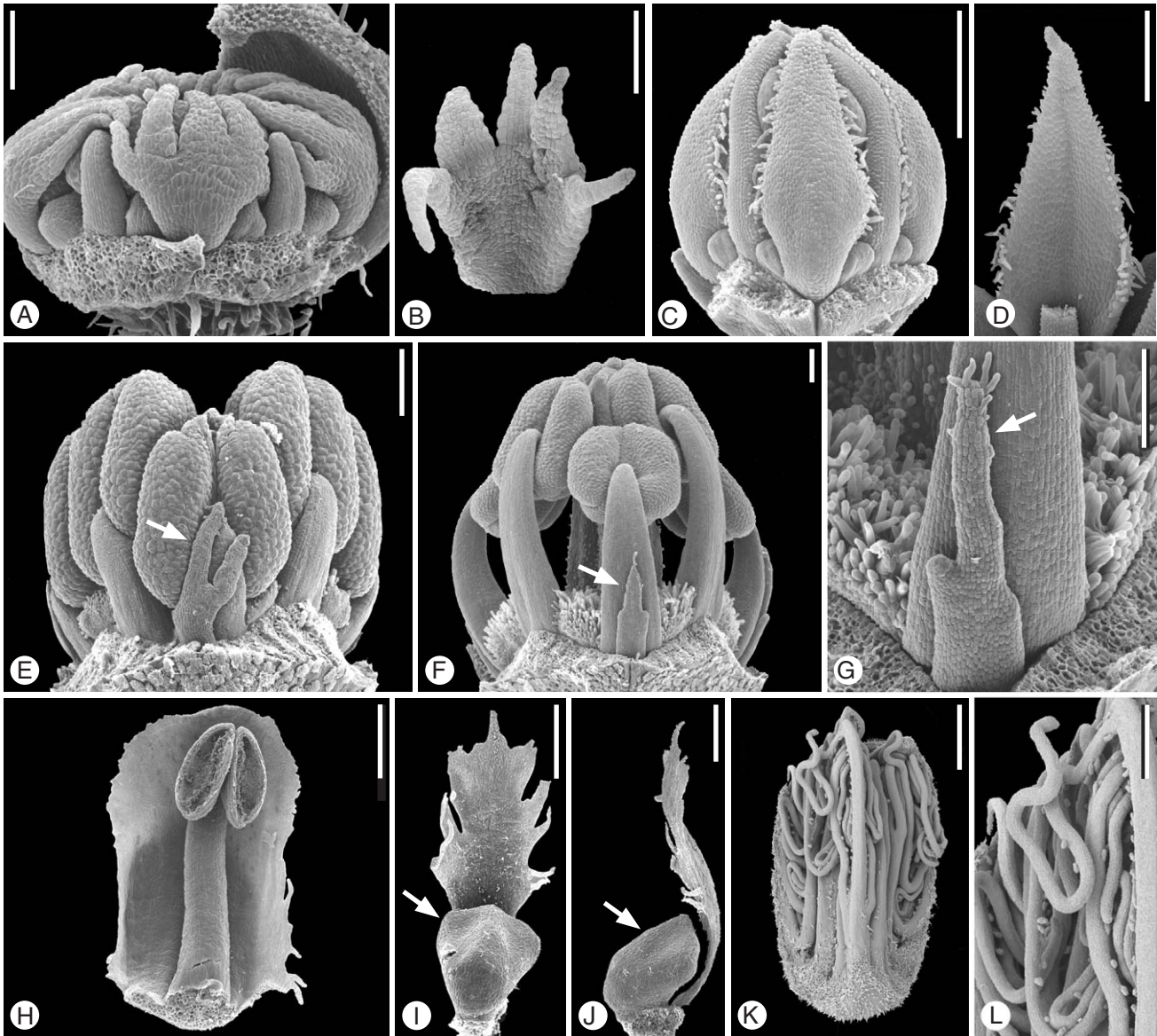


Fig. 5. Cucurbitales. (A, B) *Anisophyllea disticha* (Anisophylleaceae); (A) old floral bud, from the side, sepals partly removed; (B) petal, from ventral. (C–D) *Polygonanthus amazonicus* (Anisophylleaceae); (C) old floral bud, from the side, sepals removed; (D) petal, from ventral. (E–G) *Combretocarpus rotundatus* (Anisophylleaceae) (arrows: lobulate, reduced petals); (E) floral bud, from the side, sepals removed; (F) older floral bud, from the side, sepals removed; (G) petal from older floral bud, from dorsal. (H–J) *Corynocarpus laevigata* (Corynocarpaceae) (arrows: ventral lobes); (H) petal (plus attached stamen), from ventral; (I) staminode, from ventral; (J) staminode, from the side. (K, L) *Trichosanthes cucumerina* (Cucurbitaceae), old floral bud; (K) incurved petal, from dorsal; (L) marginal fringes, magnified. Scale bars: A, B, E–G = 0.2 mm; C, D, H–J, L = 0.5 mm; K = 1 mm.

or fringed in the radius of the petals in *Celastroidae* (*Brexia*; Engler 1930a; Matthews and Endress 2005b) (Fig. 6C) and *Hippocrateoideae* (*Helictonema*; Hallé 1990; Robson et al. 1994). In *Lophopetalum* (Celastroidae) (Loesener 1942) each petal has a three-lobed and fringed ventral scale, which may be part of the nectary disk. In *Maytenus*, the petals have longitudinal ribs on the ventral side; they form a slightly convex platform (Matthews and Endress 2005b).

In *Parnassiaceae*, some *Parnassia* species have lobed or fringed petals (e.g. *P. fimbriata*) (Simmons 2004b). The fimbriae are multicellular and filiform or flattened (Fig. 6D, E). Still more conspicuous are organs interpreted as staminodes in the same radius as the petals, and basally shortly fused with them (Daumann 1932; Ku 1987). The staminodes have a median lobe and a number of lateral ones on each side (Fig. 6F, G). In a few species (e.g. *P. palustris*) the lobes look like fingers

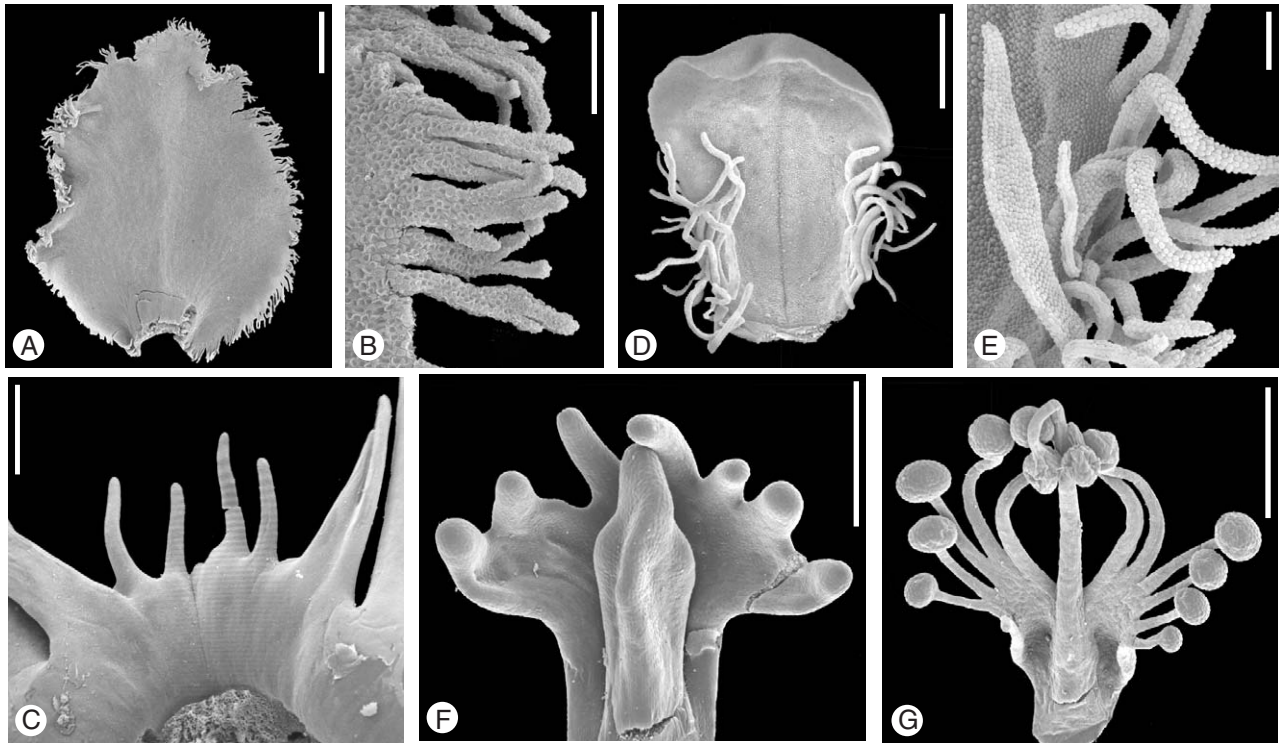


Fig. 6. Celastrales. (A, B) *Salacighia letestuana* (Celastraceae); (A) petal, from ventral; (B) petal, marginal fringes. (C) *Brexia madagascariensis* (Celastraceae), fringed nectary, from inside. (D–F) *Parnassia fimbriata* (Parnassiaceae); (D) petal, from ventral; (E) petal, marginal fringes; (F) staminode, from ventral. (G) *Parnassia palustris* (Parnassiaceae), staminode, from ventral. Scale bars: A, C, D, F, G = 1 mm; B, E = 0.2 mm.

with a conspicuously thickened, globular or pyriform apex that glistens at anthesis (Fig. 6G). In the earlier literature the globular apex was called a gland (Eichinger 1908). However, they are not secretory and the glistening effect results entirely from their smooth surface. The epidermal cells are much enlarged and each has a slightly convex surface with no or only slight cuticle ridges (see also Daumann 1932) (for their function see the section “Discussion”). Nectariferous tissue is present on the ventral side of the ‘blade’ of the staminode. In other species, such as *P. fimbriata* (Fig. 6F), the staminodes are smaller and without globular ends (Eichinger 1908; Engler 1930a).

Rosids – eurosids I – Malpighiales

Most families of Malpighiales have flowers with petals. However, petals are absent in Balanopaceae and most genera of Euphorbiaceae s.l.

Among Malpighiaceae many Neotropical genera have shortly fringed petals (e.g. *Excentradenia*, *Malpighia*; Anderson 1997). The petal fringes may be capitate and appearing glandular (e.g. *Peixotoa*; Anderson 1982). The petals may have a prominent abaxial median wing (*Malpighia*; Anderson 1987).

In Achariaceae, Pangieae have petals with a ventral appendage, which produces nectar. This was observed in *Ryparosa* (this study) (Figs. 7A, B, 13M) and *Kiggelaria* (Glück 1919; Steyn et al. 2003). According to Gilg (1925a) it is also present in *Hydnocarpus*, *Trichadenia*, *Gynocardia*, and *Pangium*.

In Dichapetalaceae, the petals are commonly bilobed (Ronse De Craene and Smets 2001) and have a simple or bilobed basal ventral nectary. It is called an antepetalous gland and interpreted as not being part of the petal by Breteler (2001). It is unclear whether originally it was a part of the petal or of an independent disk.

Euphorbiaceae s.l. in general do not have petals. However, there are structures in the flowers of a few Euphorbiaceae s.str. that should be mentioned here. *Chiropetalum* (incl. *Aonikena*) has petal-like organs that are hand-shaped with a mid-lobe (Pax and Hoffmann 1931), and *Chutia* has slightly lobed petals and lobed staminodes between the petals, the staminodial lobes being secretory (nectaries?) (Beille 1902; Pax and Hoffmann 1931; Thompson and Edwards 2001; this study) (Fig. 7C, D).

In Malesherbiaceae, a simple corona is present inside the petal whorl as a circular ridge, which may be toothed (Harms 1925a).

In Turneraceae, each petal has a ligule (*Wormskioldia*) or there is a continuous corona inside the petals (*Piriqueta*) (Gilg 1925c).

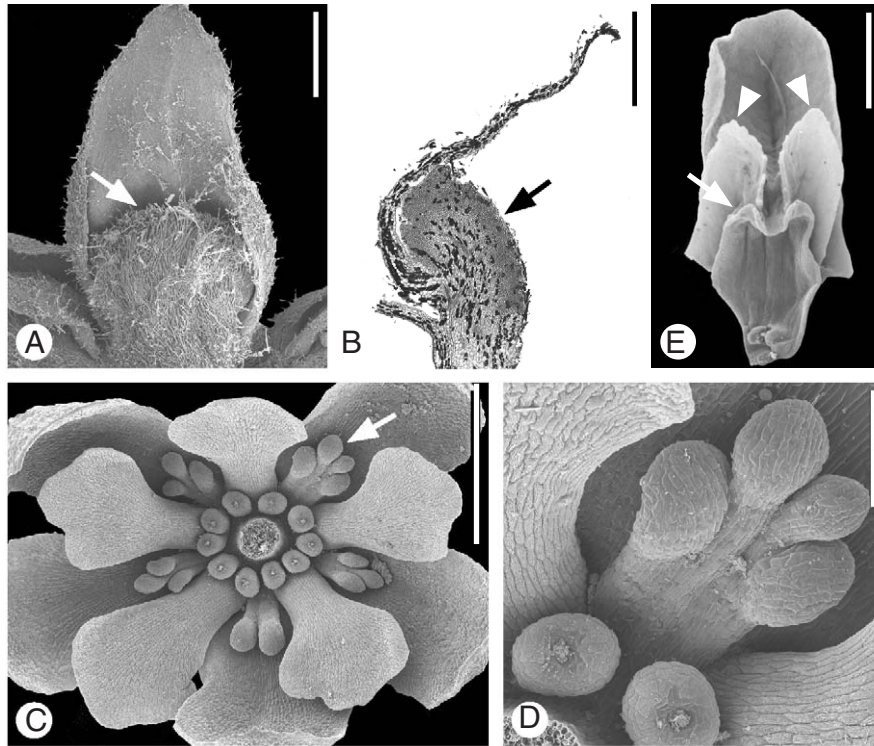


Fig. 7. Malpighiales. (A, B) *Ryparosa javanica* (Achariaceae), petal (arrows: ventral lobes); (A) from ventral; (B) longitudinal microtome section. (C, D) *Clutia* spec. (Euphorbiaceae); (C) male flower, from above, united stamens removed, with lobed petals, lobed (secretory) staminodes (arrow), and an additional series of ten secretory structures; (D) staminode with secretory lobes, from ventral. (E) *Erythroxyllum novogranatense* (Erythroxylaceae), petal, from ventral (arrow: inner ventral lobe; arrowheads: two parts of outer ventral lobe). Scale bars: A–C, E = 1 mm; D = 0.2 mm.

In Passifloraceae, some *Adenia* species have fringed petals (Harms 1925b). A simple, uniseriate corona is present (*Adenia*) (de Wilde 1974; Bernhard 1999), or a complex corona that may consist of several rings of differently shaped narrow lobes (other genera, especially *Passiflora*) (Harms 1925b; Endress 1994; Bernhard 1999). The morphological nature of the corona is not resolved. The earlier interpretation of the coronal elements as being of staminodial origin (Puri 1948, in part; Endress 1994) was questioned by Bernhard (1999), who found a very late inception of these organs, and by Krosnick and Freudenstein (2005). From the present state of knowledge it is most likely to be a new formation of the zone between petals and stamens.

In some Ochnaceae (*Blastemanthus*, *Poecilandra*, *Sauvagesia*) there are one or two rings of filamentous structures between the corolla and androecium, interpreted as staminodes (Amaral 1991). It may be asked whether these structures correspond to the corona of related families.

In *Viola* (Violaceae), the lower median petal forms a spur, which surrounds two nectaries situated at the base of two stamens (Church 1908; Smets 1986). In *Viola cazorlensis* the median petals are bilobed (Herrera 1993).

In some species of *Hypericum* and *Cratoxylum* (Hypericaceae; Chase et al. 2002; Gustafsson et al. 2002) petals have a ventral lobe (Glück 1919).

Some Linaceae have petal bases with a ventral lobe: *Hesperolinon* (Sharsmith 1961), *Roucheria* (*Hebepetalum*), and *Hugonia* (Winkler 1931). In *Hesperolinon*, in addition two lateral auricles may be present (Sharsmith 1961). Small lobes at the petal base may also be present in some species of *Linum* (Sharsmith 1961).

In Erythroxylaceae, the petals of *Nectaropetalum* (Winkler 1931; in Linaceae) and *Pinacopodium* (Exell and Mendonça 1951) have a simple ventral scale. *Erythroxyllum novogranatense* has a three-lobed ventral scale at the base of each of the five petals. An inner, median part slightly arches over the floral center as a nectar cover, while the two lateral parts are more upright and form a corona (Fig. 7E). This seems to be the common situation in the genus (Schulz 1931; Leinfellner 1954a).

Rhizophoraceae appear as sister to Erythroxylaceae (Setoguchi et al. 1999; Schwarzbach and Ricklefs 2000). In Rhizophoraceae, petal structure is by far the most diverse and most elaborate of all families described here. Therefore, we describe it in more detail than those of the

other families. Structural and functional aspects were studied by Tomlinson (1986), Juncosa and Tomlinson (1987, 1989b), and Juncosa (1988).

Here, some additional new observations are presented. The petals are more or less conduplicate in most genera and have a robust consistency in several genera. Towards the apex they have a median and often several lateral appendages. The median appendage is sometimes especially pronounced and is termed an “arista” (Juncosa 1988). The conduplicate shape may result in a bifid appearance of the petal (Juncosa and Tomlinson 1989b). Each petal may embrace one to several stamens. In a first clade, Rhizophoreae (all mangrove plants, whereas all other Rhizophoraceae are non-mangrove plants), the petal apex and the subdivisions are commonly straight and directed upward in bud; the subdivisions themselves may be long or much reduced and almost obliterated at anthesis. In a second clade, Gynotrocheae, the petal apex and/or subdivisions are incurved in bud. In a third clade, Macarisieae (which is sister to the first two clades), the petals are less uniform.

The first clade, Rhizophoreae, has the most elaborate petals. In *Bruguiera gymnorhiza* the petals are strongly bifid and in bud they are conduplicate like a bivalve (Fig. 8A). Apart from the (median) arista there are three terminal bristles on each side (Fig. 8A, B). The bristles (including the arista) have slightly thickened ends (containing transfusion tissue with tracheoids). Each petal tightly encloses two stamens (the antepetalous one of the same radius and one of the two adjoining alternipetalous ones; see Juncosa and Tomlinson 1987) by postgenital union of the margins. This bond is explosively released when the petal base in the open flower is touched, a result of the two petal halves being under tension (Davey 1975; see also Gehrman 1911 for *B. eriopetala*). The petal flanks show a ridged sculpture on the outside (dorsal surface), which is directed obliquely upward from the midline to the margins and may be the cause of the tension (Fig. 8C, D). In the relaxed state the formerly united areas show longitudinal folds that were locked together like in a zipper. In *B. cylindrica* the petals are smaller but similar in structure (Fig. 8E–L). In *B. exaristata* the petals are bifid but devoid of bristles, and the median arista is very short (Ding Hou 1958). In *Ceriops tagal* the petals are also bifid and each flank has one or two short terminal bristles and a median arista, which is, however, less dorsally displaced than in *Bruguiera* (Fig. 8M–O). One or two additional bristles may also be present as rudimentary humps (see also Juncosa and Tomlinson 1987) (Fig. 8N). The bristles (including arista) are thickened at the end and contain transfusion tissue with tracheoids. As in *Bruguiera*, the opposing inner margins of each petal are held together before triggering by interlocking surface ridges (Juncosa and Tomlinson 1987). Only one stamen, the corresponding antepetalous

one, is enclosed in the petal. In the lower half of each petal there is a short zone where the margins of adjacent petals are held together by helically coiled hairs (Juncosa and Tomlinson 1987) (Fig. 8P–R). *Ceriops decandra* differs from *C. tagal* in that the terminal bristles on each side of the petal are shorter but greater in number (about seven on each side) and are slightly incurved in bud. Each contains a nest of tracheoids and, in addition, a hydathode in the epidermis (Juncosa and Tomlinson 1987). In the lower half of the petals the margins bear short hairs. However, in contrast to *C. tagal* they are not tightly coiled but rather uncinat and irregularly curved. The petals of *Kandelia* resemble those of *Bruguiera* (Ding Hou 1958).

In the second clade, Gynotrocheae, the two genera with the most similar petals (by their terete and vermicular lobes), *Gynotroches* and *Pellacalyx*, appear as sisters in morphological and molecular analyses (Juncosa 1988; Juncosa and Tomlinson 1989b; Schwarzbach and Ricklefs 2000). *Gynotroches*, *Pellacalyx*, and *Carallia* share petals with a large number of multicellular lateral appendages. The petals are more or less conduplicate; a terminal appendage (arista) is also present. The petals are apically bilobed in *Gynotroches* but less clearly so in the other taxa. In *Gynotroches axillaris*, the appendages on each lobe are terete and vermicular; on the dorsal side the petals (and appendages) bear scattered long, unicellular hairs, often with a hooked end (Fig. 9A–C). In *Pellacalyx cristatus*, the appendages (about 6 or more on each side) are also terete and vermicular but slightly thickened at the end; the dorsal side of the petals is densely covered with unicellular hairs (Fig. 9D–F). In *Carallia borneensis*, the appendages are of irregular shapes, somewhat flattened, some incurved, some recurved (Fig. 9G–I).

In the third clade, Macarisieae, *Cassipourea pumila* has petals with broad, leaf-like appendages (Flore 1988). In *Cassipourea* spec., the appendages are covered with flattened unicellular hairs, which may be easily mobile (this study) (Fig. 9J–L). *Macarisia* has numerous irregular appendages on each petal (Schimper 1893). In *Sterigmaphetalum* petals, a three-lobed middle part is flanked by two lateral flanges, each with 2–18 appendages (Steyermark and Liesner 1983). An additional (monotypic) genus, *Comiphyton*, which was not included in phylogenetic analyses, has petals with 5–6 short lobes (Flore 1974).

In *Crossostylis* (Gynotrocheae) and *Rhizophora* (Rhizophoreae) the petals are straight in bud and the subdivisions are only rudimentary in adult flowers. In *Crossostylis grandiflora*, three lobes, a median flanked by two lateral ones, are prominent in young buds (Fig. 9M). However, they cease to grow early in development, and in adult flowers they are restricted to the very tip of the petal (Fig. 9N). According to Juncosa and Tomlinson (1989b) marginal petal

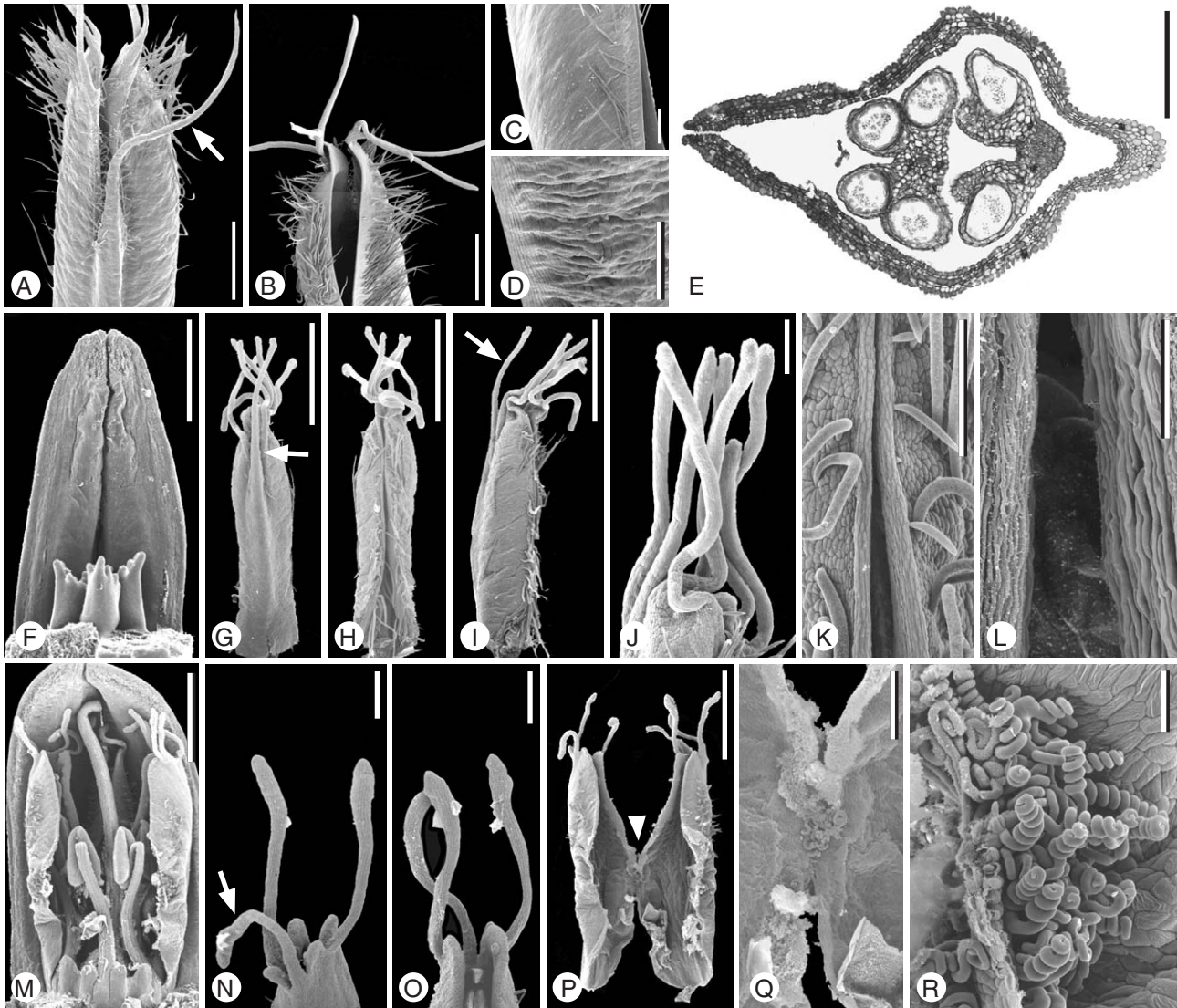


Fig. 8. Rhizophoraceae. (A–D) *Bruguiera gymnorhiza*; (A) petal, from dorsal (arrow: arista); (B) petal, from ventral; (C) petal flank, from the side; (D) petal flank, from the side, with oblique furrows. (E–L) *Bruguiera cylindrica*; (E) petal of a bud, embracing two stamens, transverse microtome section; (F) young floral bud, showing two sepals and three petals; (G) petal, from dorsal (arrow: arista); (H) petal, from ventral; (I) petal, from the side (arrow: arista); (J) petal tip, from the side; (K) coherence of petal flanks, lower ventral side; (L) petal flanks with epidermal longitudinal ridges in region of coherence. (M–R) *Ceriops tagal*; (M) floral bud, from the side, perianth partly removed; (N) petal tip, from dorsal (arrow: arista); (O) petal tip, from ventral; (P) two petals coherent by their flanks (arrowhead), from ventral; (Q) region of petal coherence; (R) coiled hairs at region of coherence. Scale bars: A, B, G–I, M, P = 1 mm; C, F = 0.5 mm; D, E, J, K, N, O, Q = 0.2 mm; L = 0.025 mm; R = 0.05 mm.

appendages are absent in *Rhizophora*. However, we found three tips on the petals in *Rhizophora* × *lamarckii* (Fig. 9O). In *R.* cf. *mucronata* and *R. stylosa* the petals are densely covered with hairs on the dorsal side, so that their apices are difficult to study. *Crossostylis grandiflora*, in addition, has protuberances and tufts of long unicellular hairs inside the stamens. They appear to function as retainers for nectar produced by nectaries towards the floral center of the pendant flowers (Juncosa 1988). *Anopyxis* (not included in molecular analyses) also has petals with three apical teeth (Sprague and Boodle 1909).

Rosids – eurosids I – Oxalidales

Petals are absent in Brunelliaceae and Cephalotaceae, present or absent in Cunoniaceae and Elaeocarpaceae, or even within a genus as in *Ceratopetalum* and *Codia* (Cunoniaceae) (Rozefelds and Barnes 2002; Bradford et al. 2004) and *Sloanea* (Elaeocarpaceae) (Coode 2004). Among Connaraceae the petals may be slightly lobulate in *Cnestis* (Matthews and Endress 2002). Among Oxalidaceae, staminodes are trilobed in *Averrhoa* (Fig. 10M). In some Cunoniaceae and in Elaeocarpaceae the petals are conspicuously subdivided.

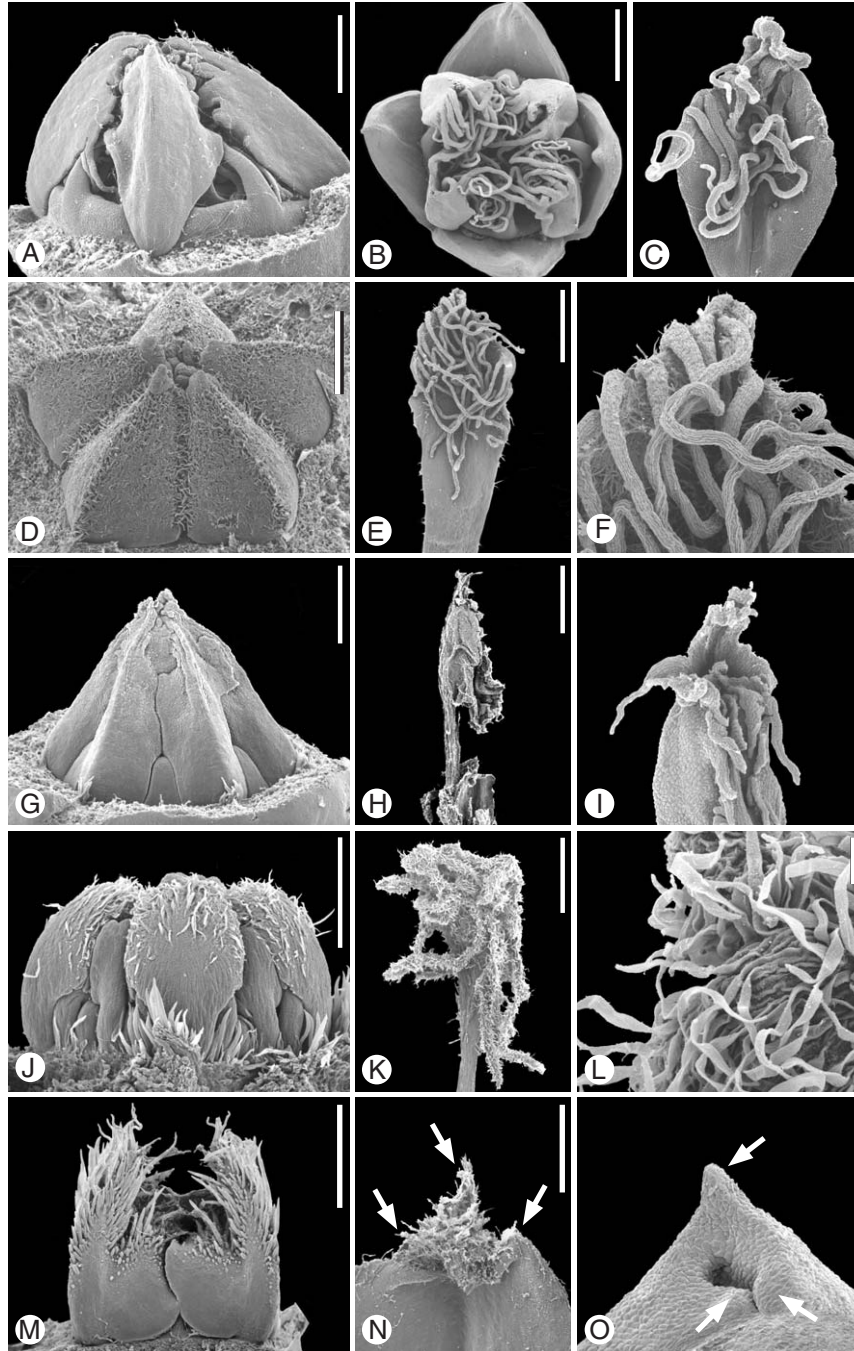


Fig. 9. Rhizophoraceae. (A–C) *Gynotroches axillaris*; (A) floral bud, from the side, sepals removed; (B) flower, from above; (C) petal, from ventral. (D–F) *Pellacalyx cristatus*; (D) floral bud, from the side, sepals removed; (E) petal, from ventral; (F) petal tip, from ventral. (G–I) *Carallia borneensis*; (G) floral bud, from the side, sepals removed; (H) petal, from the side; (I) petal tip, from the side. (J–L) *Cassipourea* spec.; (J) floral bud, from the side, sepals removed; (K) petal, from ventral; (L) hairs on the petal fringes. (M, N) *Crossostylis grandiflora*; (M) petals of young floral bud; (N) tip of petal of old floral bud, from ventral (arrows: reduced petal lobes). (O) *Rhizophora* × *lamarckii*, tip of petal of old floral bud, from ventral (arrows: reduced petal lobes). Scale bars: A, C, D, F, G, I, J, M = 0.5 mm; B, E, H, K, N = 1 mm; L = 0.05 mm; O = 0.1 mm.

In Cunoniaceae, petals are absent in more than half of the genera; if present they are generally small. Of the ten petaliferous genera, five are reported to have divided (ternate) petals: *Schizomeria*, *Ceratopetalum*, *Platylophus*, *Gillbeea*, and *Anodopetalum* (Engler 1930b; Mat-

thews et al. 2001; Matthews and Endress 2002). In *Schizomeria*, *Ceratopetalum* and *Platylophus* there is a middle and two or more lateral lobes; the lobes are flat and tapering. *Anodopetalum* petals are very shortly trilobed at the tip, as evident from the figures in Barnes

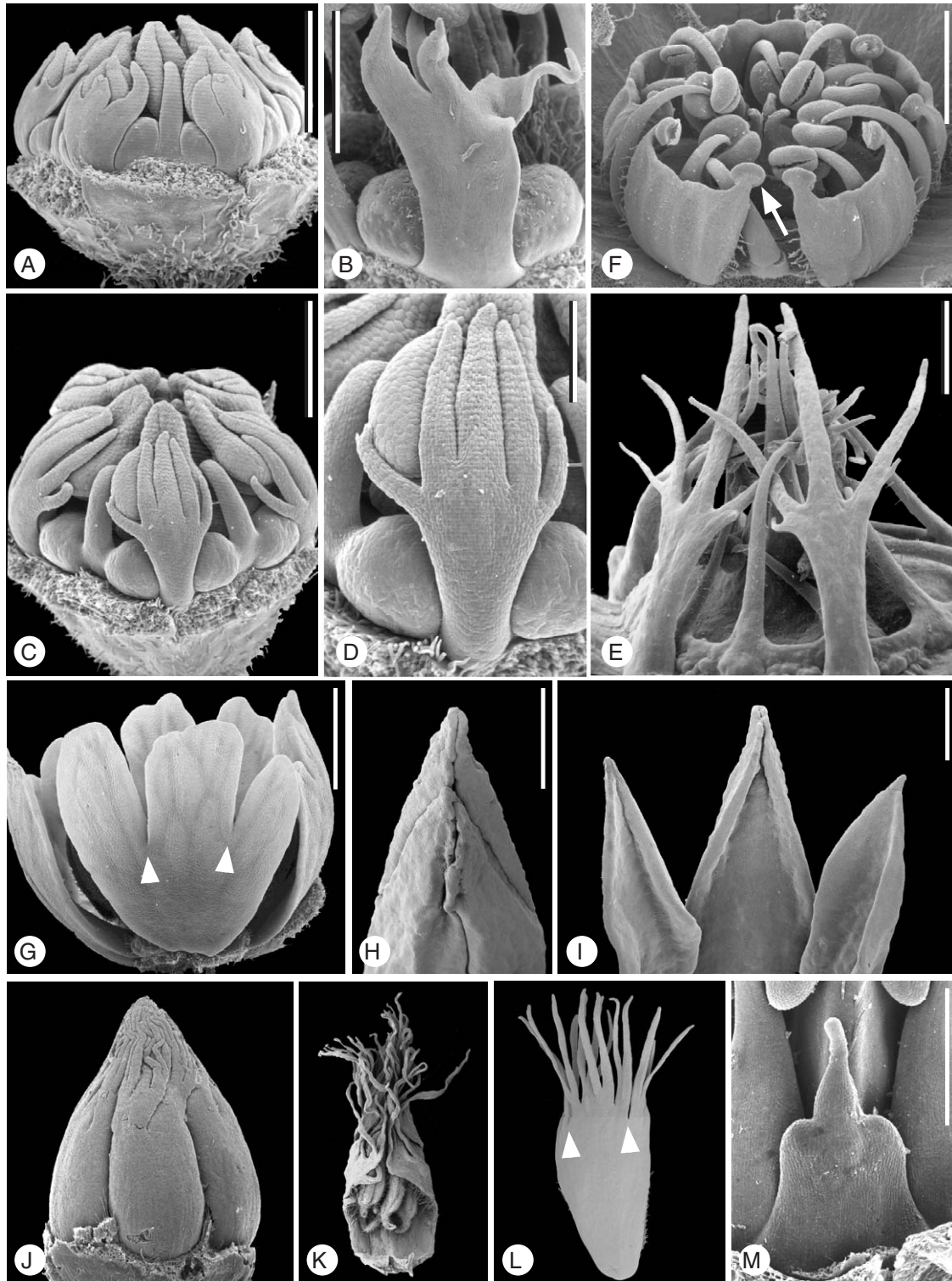


Fig. 10. Oxalidales. (A, B) *Schizomeria whitei* (Cunoniaceae); (A) floral bud, from the side, sepals removed; (B) petal, from dorsal. (C–E) *Ceratopetalum gummiferum* (Cunoniaceae); (C) floral bud, from the side, sepals removed; (D) petal of bud, from dorsal; (E) petals, from dorsal. (F) *Gillbeea adenopetala* (Cunoniaceae), floral bud, sepals removed, showing petals with two thickened lobes (arrow). (G) *Aristotelia serrata* (Elaeocarpaceae), flower, from the side (arrowheads: deepest incisions). (H, I) *Crinodendron patagua* (Elaeocarpaceae); (H) petal tip of bud, from ventral; (I) petal tip, from ventral. (J, K) *Elaeocarpus* cf. *subvillosus* (Elaeocarpaceae); (J) floral bud, from the side, sepals removed; (K) petal from bud, embracing several stamens. (L) *E. reticulatus* (Elaeocarpaceae), petal, from dorsal (arrowheads: deepest incisions). (M) *Averrhoa carambola* (Oxalidaceae), lobed staminode, from dorsal. Scale bars: A, B, E–L = 1 mm; C, M = 0.5 mm; D = 0.2 mm.

and Rozefelds (2000). Of the taxa investigated here, *Schizomeria* has petals with commonly three lobes that have about the same proportions in mid-sized buds as at anthesis (Fig. 10A, B). *Ceratopetalum* has petals with five lobes. In small buds they are already well developed, and the petal is hand-shaped (Fig. 10C, D). At anthesis, the five lobes are proportionately much longer and thinner, as compared with the entire petal shape (Fig. 10E). The Oligocene fossil *Schizomeria tasmaniensis* has bi- to trilobed petals (Carpenter and Buchanan 1993). In contrast, *Gillbeea* has only two lateral lobes and no median one, and the lobes have a thickened knob (Fig. 10F). This difference in structure is also reflected in their phylogenetic relationships: *Schizomeria*, *Ceratopetalum*, *Platylophus* and *Anodopetalum* appear in a clade (sect. Schizomerieae), *Gillbeea* appears more isolated (Bradford and Barnes 2001). In *Gillbeea*, the two thickened knobs function as a gland at anthesis (Endress 1994; Rozefelds and Pellow 2000). They have a secretory epithelium and are served by a vascular bundle. Anthetic flowers observed in the field showed that the two knobs of each petal glisten. This glistening effect comes about by the presence of an exudate covering the knob. It is (at least partly) insoluble in water and alcohol. An untested hypothesis is that the petal knobs act as pseudonectaries and optically attract pollinators to the real nectar, which is produced in the floral center by a disk nectary around the gynoecium (see the section “Discussion” below and Endress 1994). The petals are already crescent-shaped in small buds.

Elaeocarpaceae are petaliferous except for part of the genus *Sloanea* (Coode 2004). In more than half of the genera the petals are divided (Matthews and Endress 2002; Coode 2004). They are not divided in the former Tremandraceae, which are now included in Elaeocarpaceae (Coode 2004). The divided petals either simply have three lobes (e.g. *Vallea*, *Aristotelia*, *Crinodendron*, *Peripentadenia*; Coode 2004) or the three primary lobes are subdivided into numerous secondary lobes (e.g. *Peripentadenia*; Coode 1988; and *Elaeocarpus*; Coode 1984, 2001). *Aristotelia serrata* has flat petals with three or four broad lobes and with imbricate aestivation of the lobes (Fig. 10G). In *Crinodendron hookerianum* and *C. patagua* the petals also have three apical lobes. However, they are induplicative-valvate, whereby the median part and the two lateral incurved parts are each terminated by one of the three lobes (Fig. 10H, I). In addition, each of the three lobes is induplicative in itself (at least in *C. patagua*) (Fig. 10I). Each petal embraces more than one stamen in bud. In *Elaeocarpus* the petals are multiply lacinate at the apex, and each petal embraces several stamens in bud (Fig. 10J–L) (Rao 1953; Matthews and Endress 2002). In some taxa petals have a basal pouch (Coode 2004).

Rosids – eurosids II – Brassicales

In the largest clade of Brassicales (Brassicaceae, Cleomaceae, Capparaceae) (Hall et al. 2002) elaborate petals are almost absent. In Capparaceae petals are present or absent. Among Brassicaceae, *Chlorocrambe*, *Dryopetalon* and *Schizopetalon* have petals with several lobes, including a mid-lobe; a number of genera have bilobed petals (e.g. *Alyssum*, *Erophila*) (Schulz 1936). Among Cleomaceae, *Cleome* sect. *Cleome* subsect. *Simplicifoliae* has petals with a ventral scale at the base of the blade, which is connected to the petal margins, thus making the petal peltate (Guédès 1968); *Polanisia* has simple, bilobed or trilobed petals that may be secondarily subdivided (Iltis 1958); *Cristatella* has petals with several lobes (Pax and Hoffmann 1936). Among Capparaceae, *Ritchiea* (*R. macrantha*) may have bi- to trilobed petals (Kers 1987).

In Emblingiaceae, petals of *Emblingia* have two narrow, ribbon-like appendages on their ventral side (Leins 1969). Some Limnanthaceae have slightly bilobed petals.

In some families of Brassicales, cucullate petals are present. However, these families do not form a clade in the *rbcL* study by Savolainen et al. (2000).

In Pentadiplandraceae, petals of *Pentadiplandra* are basally cucullate, covering a nectary disc (Ronse De Craene 2002).

Among Resedaceae petals are lobed in *Oligomeris*. They are highly lobed and with a ventral scale and a cucullate base covering the nectary disk in *Reseda*, *Caylusea*, *Astrocarpus* (Bolte 1936; Sobick 1983) (Fig. 11A); they are ternate (von Gumpenberg 1924). In contrast, petals are lacking in *Ochradenus* (Bolte 1936). *Randonia* is said to have a double disk, with the inner one denticulate, often whitish and similar to the claw of the petals (Bolte 1936). Anatomical as well as developmental studies have been made in *Reseda* (Müller 1893; von Gumpenberg 1924; Bolte 1936; Baum 1950, 1951; Sobick 1983): the mid-lobe of the trilobed petals in *R. luteola* is precocious, the lateral lobes retarded (Baum 1951).

In Tropaeolaceae, lobed petals occur in a number of *Tropaeolum* species (Farenholtz 1931; Sparre and Andersson 1991). There is a diversity of forms: simply bilobed, trilobed with secondary subdivisions, and without major primary lobation, but with many small lobes or teeth (Huynh 1968). The petals may also be basally peltate (Baum 1950). The upper and lower petals of the monosymmetric flowers differ in shape. In *T. peregrinum* the lower petals are small and narrow with linear lobes, while the upper ones are much larger and broader, with broader lobes (Fig. 11B). The lobes may be directed in such a way as to restrict access to the floral center (e.g. *T. majus*), but detailed studies are lacking.

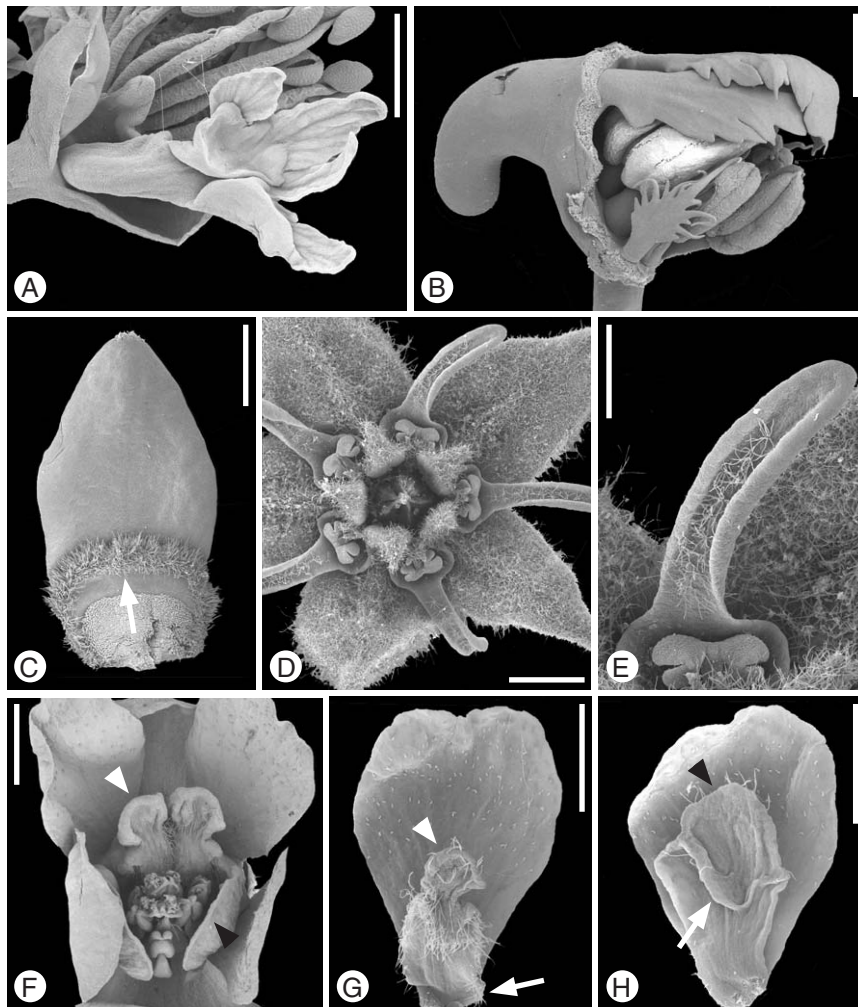


Fig. 11. Brassicales, Malvales, and Sapindales. (A) *Reseda luteola* (Resedaceae), flower, from the side, with petal from dorsal. (B) *Tropaeolum peregrinum* (Tropaeolaceae), floral bud, from the side, sepals partly removed. (C) *Grewia crenata* (Malvaceae), petal, from ventral (arrow: ventral lobe). (D, E) *Commersonia fraseri* (Malvaceae); (D) flower, from above; (E) petal, from ventral. (F–H) *Cardiospermum halicacabum* (Sapindaceae); (F) flower, from above (white arrowhead: ventral lobe of upper petal; black arrowhead: ventral lobe of lower petal); (G) upper petal, from ventral (arrow: lower ventral lobe; arrowhead: upper ventral lobe); (H) lower petal, from ventral (arrow: lower ventral lobe; arrowhead: upper ventral lobe). Scale bars: A–D, F–H = 1 mm; E = 0.5 mm.

Rosids – eurosids II – Malvales

Most Malvaceae have petals, but they are lacking in Sterculioideae, and occasionally in Byttnerioideae–Lasiopetaleae, Bombacoideae, and Helicteroideae–Durioideae. In Grewioideae, in some genera, such as *Grewia* and *Goethalsia*, petals with a cucullate base contain a ventral nectary that is covered by the hairy upper rim of the cucullate part (Figs. 11C, 13K) (Capuron and Mabberley 1999; Vogel 2000; Bayer and Kubitzki 2002) (Fig. 11C). Two interesting variants of this pattern demonstrate how architectural elements can transgress morphological units: (1) the nectary is slightly displaced from the petal base to the androgynophore, but the petal remains cucullate and still covers the nectary, e.g., in *Corchorus* and *Triumfetta* (Fig. 13L) (Vogel 2000;

Leitão et al. 2005); (2) the nectary remains on the petal base, but the latter is not cucullate and the nectar cover is formed by a whorl of lacinate staminodes, e.g., in *Luehea* (Vogel 2000).

In Byttnerioideae, the petals are basally cucullate, enclosing stamens, and sometimes a distinct ventral lobe is present at the upper end of the cucullate part (Cristóbal 1960, 1976; Leinfellner 1960; Bayer and Hoppe 1990; Whitlock et al. 2001; Bayer and Kubitzki 2002). In *Guazuma* the upper part of the petals (above the cucullate base) is deeply bilobed; in other genera it is reduced (Leinfellner 1960; Bayer and Kubitzki 2002). In some genera, the petals appear trilobed because the lower part has two lateral lobes at its upper end (e.g. species of *Ayenia*, *Commersonia*) (Fig. 11D, E). In *Ayenia*, the lower part of the petals is not cucullate,

instead it has a long stalk and a broadly expanded plate, and the upper part forms only a short appendage. The five expanded plates are postgenitally coherent so that the flower attains a gracile, lantern-like shape with five lateral entrances (figures in Cristóbal 1960).

In Helicteroideae, petals are similarly but less conspicuously differentiated into a lower and an upper part (Bayer and Kubitzki 2002).

In some Tilioideae (species of *Tilia*) the petals have a basal ventral scale (Glück 1919).

In Malvoideae, petals are commonly not especially elaborate. Some taxa have bilobed petals, such as species of *Malva* and *Sidalcea*. *Hibiscus schizopetalus*, as an exception, has pinnately lobed petals.

Thymelaeaceae commonly lack petals. However, *Dicranolepis* has lobed petals (Vogel 1954). Whether the “annulus” in *Stephanodaphne* (Rogers 2004) also corresponds to a ring of lobed petals is unclear.

Rosids – eurosids II – Sapindales

Except for Sapindaceae, there are few petal elaborations in Sapindales. In Rutaceae, *Spiranthera odoratissima* has disk lobes with appendages (Engler 1926). In Anacardiaceae, *Mangifera* has longitudinal ribs on the basal part of the ventral petal surface (e.g. Endress 1994).

In Sapindaceae (incl. Hippocastanaceae), petals with a radially divided ventral scale are common (Radlkofer 1896; Baum 1950; Leinfellner 1955, 1958; Reynolds and West 1985; Adema et al. 1994). *Cardiospermum halicacabum* has monosymmetric flowers with two pairs of lateral petals. Each petal has a two-lobed ventral scale at its base. The scale is more conspicuous in the petals of the upper pair. An inner (ventral), median part slightly arches over the floral center as a nectar cover (Fig. 13H); the outer median part is more upright, forming a paracorolla and nectar guide in having a yellow mark (Fig. 11F, G). The lower pair does not exhibit contrasting colors (Fig. 11H). This pattern is common in many genera. Petal elaborations are diverse in detail in Sapindaceae, which is suggested by the work of Radlkofer (1896) but has not been comparatively elucidated.

Asterids – Cornales

In Cornaceae, the petals (and also the stamens) of *Alangium* (*A. circulare*) have slightly cucullate bases, which together form a chamber over the nectary disc (Stone and Kochummen 1975).

Among Loasaceae, *Fuertesia domingensis* (Gronovioideae) has lobed petals with a mid-lobe and several side lobes; the lobes are incurved in bud (Moody and Hufford 2000; Weigend 2000). Loasoideae have a ‘corona’ consisting of five organs alternating with the five petals, often conspicuous by their bright colors, each

covering a nectary with its concave inner side, thus forming revolver flowers. These organs may be subdivided and are diverse in shape; each organ corresponds to a group of united staminodes (Gilg 1925b; Leins and Winhard 1973; Hufford 2003; Weigend et al. 2004). In *Blumenbachia* they have three multicellular terete appendages on the basal dorsal side (Fig. 12A, B). In *Nasa*, each organ has two apical horns (Fig. 12C). In both genera the organs have tangentially directed zones of different surface structure and color, as is suggestive of “roundabout flowers” (see Endress 1994).

Asterids – Ericales

In the highly monosymmetric flowers of Balsaminaeae, some species of *Impatiens* have petals with two or more lobes, e.g. *I. scapiflora* and *I. capensis* (Vogel 1954; Grey-Wilson 1980).

The clade consisting of the former Ebenales and Primulales (Schönenberger et al. 2005) exhibits some diversity in lobed petals and staminodes. Sapotaceae commonly have more than one organ whorl between sepals and stamens. However, because these organs are congenitally fused, both among and between whorls, their delimitation is sometimes difficult. The petals have been interpreted as trilobed in several genera (Aubréville 1961). In addition, there is at least one whorl of subdivided staminodes in a number of genera (Aubréville 1961). In *Mimusops commersonii*, there are 16 lacinate staminodes in one whorl and eight entire staminodes in a second whorl, located between the corolla and androecium (Fig. 12D). Among Primulaceae, commonly *Primula* has bilobed petals (Thenen 1911); several species have shortly dentate petals; an exception is *P. deuteronana*, which has trilobed petals (Richards 2003). Bilobed petals are also present in some *Androsace* species (Thenen 1911). The petals of *Soldanella* are conspicuously lobed, and apparently basically trilobed (Thenen 1911; Zhang and Kadereit 2003). Among Theophrastaceae, *Jacquinia* may have shortly bilobed staminodes (e.g. *Jacquinia keyensis*) (Walker-Larsen and Harder 2000).

In Polemoniaceae, petals are rarely bilobed (species of *Phlox*, *Microsteris*; Grant 1959). Trilobed petals are present in *Gilia triodon*, denticulate petals in *Linanthus dianthiflorus*. Petals have ventral scales in *Gilia parryae* (Brand 1913).

In the core Ericales, in Diapensiaceae there are conspicuously lacinate petals in *Shortia* (Rönblom and Anderberg 2002). It is not clear whether they have a simple, binate or ternate pattern. In Ericaceae, *Enkianthus cernuus* has deeply lacinate petals (Anderberg 1994). In *Acrotriche serrulata* (epacridoid Ericaceae), petals bear subterminal tufts of hairs that act as pollen presenters (McConchie et al. 1986).

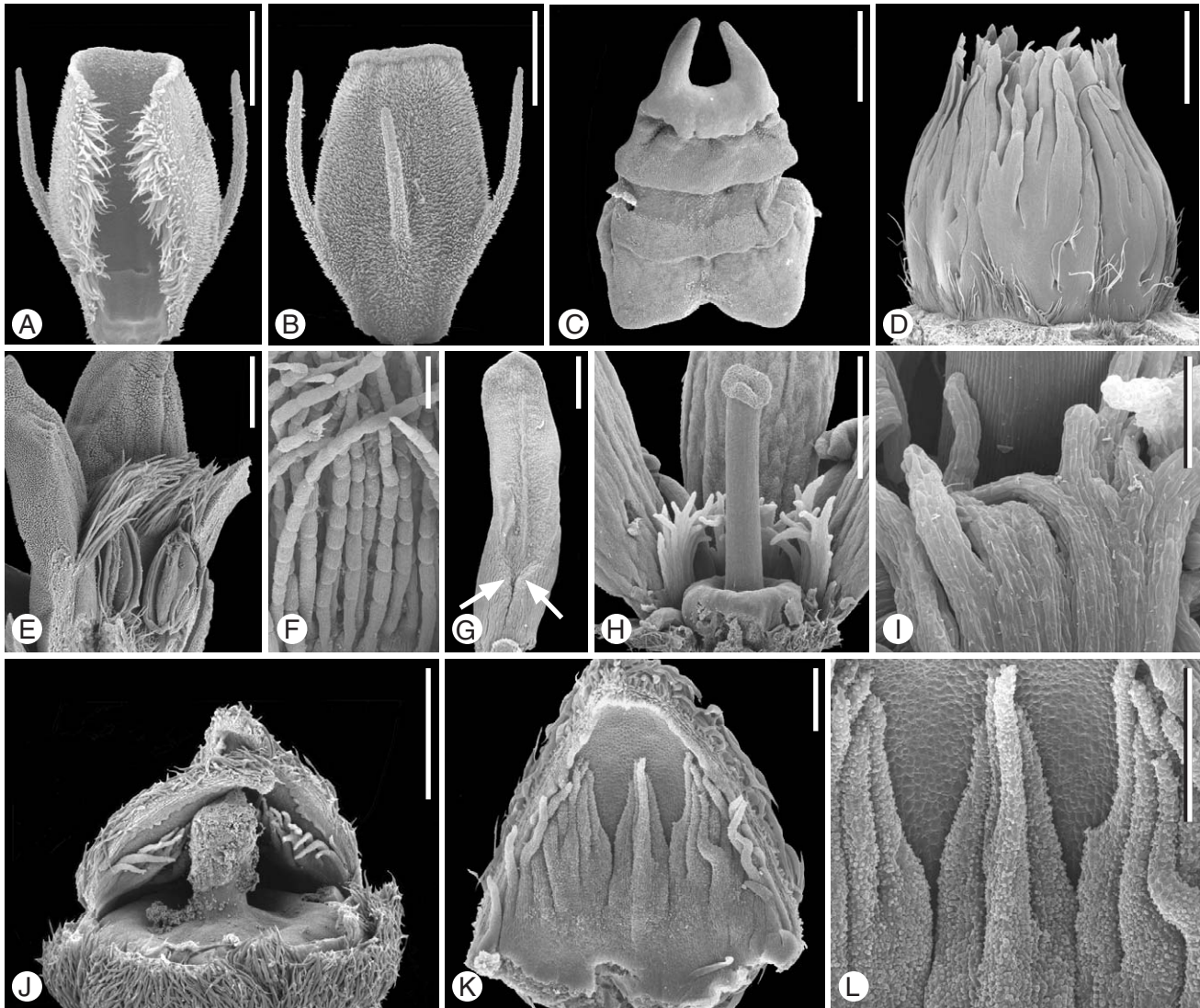


Fig. 12. Asterids. (A–B) *Blumenbachia hieronymyi* (Loasaceae); (A) staminodial scale, from ventral; (B) staminodial scale, from dorsal. (C) *Nasa triphylla* (Loasaceae), staminodial scale, from dorsal. (D) *Mimusops commersonii* (Sapotaceae), floral bud, sepals and petals removed, showing fringed staminodes. (E, F) *Neuburgia celebica* (Loganiaceae); (E) part of flower, showing tufts of hairs at floral entrance; (F) moniliform hairs of tuft. (G) *Berzelia lanuginosa* (Bruniaceae), petal, from ventral (arrows: ventral lobes). (H, I) *Corokia cotoneaster* (Argophyllaceae); (H) flower, from the side, part of the floral organs removed; (I) fringed ventral lobe of a petal, from dorsal. (J–L) *Argophyllum cryptophlebium* (Argophyllaceae); (J) flower bud, from the side, part of the floral organs removed; (K) petal of bud, from ventral, showing fringed ventral lobe. (L) ventral lobe with fringes, from ventral. Scale bars: A–E, H, J = 1 mm; F, G, I, K, L = 0.2 mm.

Asterids – euasterids I – Gentianales

Gentianaceae have an evolutionarily plastic corolla with several possibilities for modifications. In *Gentiana* (Gentianinae) the free parts of the petals alternate with smaller lobes that are situated in the folded areas of the contorted corolla and thus form a corona (paracorolla); these lobes can be variously fringed or lobed (Halda 1996). In *Crawfordia* and *Tripterospermum* the lobes are denticulate (Hul 2002). In Swertiinae, petals may be fringed at the margin (*Gentianopsis*) or they may have fringes on the ventral surface, which may be associated

with the double nectaries present on each petal (*Swertia*, *Frasera*) or positioned at the entrance of the salverform flowers (*Gentianella*) (von Hagen and Kadereit 2001, 2002; Kadereit and von Hagen 2003). These fringes may also be seen as a kind of a paracorolla. In *Halenia*, each petal has a spur containing the nectaries.

In Loganiaceae (e.g. *Neuburgia*, *Polypremum*) there are tufts of moniliform (uniseriate) hairs at the floral entrance on the ventral side of the petals (Fig. 12E, F). Such a rim of hairs is also present in some Apocynaceae (e.g. *Rauwolfia*; Schumann 1895).

In some Apocynaceae–Asclepiadoideae the petals have a conspicuous terminal appendage (e.g. species of *Ceropegia*, *Trichosacme*) (Nelson 1954; Vogel 2001). The most complex floral architecture is present in species of *Ceropegia*, in which the petals together form a pagoda-like structure with five lateral entrances (*C. sandersonii*), or in addition a central antenna with an osmophore flag (*C. distincta*) (Vogel 1961, 2001; Endress 1994). The single petals have elaborate shapes. In *Ceropegia* and other genera, the petals also often have vibratile hairs. In Apocynaceae, the corona (paracorolla) is a conspicuous feature of the complicated flowers of Asclepiadoideae and Periplocoideae. It is situated between the corolla and the androecium. However, a corona is also present in representatives of Rauvolfioideae (e.g. *Melodinus*) and Apocynoideae (e.g. *Nerium*, *Strophanthus*). The corona seems to have its evolutionary origin in the corolla (Fallen 1986). A survey on the diversity of the corona in Apocynaceae s.l. is given in Endress and Bruyns (2000). An evolutionary study of the origin of coronas throughout the Gentianales would also be of interest.

Among Rubiaceae, a conspicuous appendage at the petal tip is present in *Corynanthe*, *Hutchinsonia*, and *Pausinystalia* (Robbrecht 1988; Stoffelen et al. 1996); the appendage is bilobed in *Joosia* (Schumann 1897). Trilobed petals occur in *Dentella* (Schumann 1897) and *Spermacoce*, in the extreme case with two long lateral lobes (Harwood and Dessein 2005). In some Cinchoneae petals are fringed (Robbrecht 1988). In a number of genera the corolla tube has a ring of hairs at the entrance (e.g. species of *Borreria*, *Hedyotis*, *Pentodon*, *Psychotria*, *Randia*). In *Rondeletia odorata* there is a ring-shaped ridge at this site (Baum 1950).

Asterids – euasterids I – Boraginaceae

Boraginaceae (including Hydrophyllaceae) often have a series of hollow scales (like spurs, but protruding on the ventral side) at the entrance to the floral tube (especially prominent in *Symphytum*) (Arber 1939). Some *Cordia* species have bilobed petals (Taroda and Gibbs 1986). *Phacelia fimbriata* has fimbriate petals. In many genera two longitudinal flanges are present on the ventral base of the petals, flanking the stamen filaments (Brand 1913; Hofmann 1999). In *Hydrocera*, petals are lobulate (Cook 1996). In *Hilsenbergia schatziana* the small petals are lobulate, whereas in *H. apetala*, the corolla is reduced to a small ring (Miller 2003).

Asterids – euasterids I – Lamiales

Compared to the large number of genera and species in Lamiales, relatively few taxa have elaborate petals. Bilobed petals occur, for example, in *Thunbergia* species (Acanthaceae), *Tabebuja lepidota* (Bignoniaceae), in

Jamesbrittenia and *Zaluzianskya* (Manuleae, Scrophulariaceae) (Hilliard 1994), *Mimulus* (Phrymaceae), and in *Euphrasia* (Orobanchaceae). In *Zaluzianskya* (Scrophulariaceae) doubly bilobed petals also occur (Troll 1928). More complicated petals with several lobes or fringes occur rarely and are scattered across several families, such as Bignoniaceae (*Stereospermum fimbriatum*; Gardner et al. 2000), Gesneriaceae (species of *Drymonia*, *Episcia*, *Paradrymonia*; Wiehler 1983; *Schistolobos*; Ying et al. 1993), Lamiaceae (*Becium*; Williamson and Balkwill 1995; *Collinsonia*), Lentibulariaceae (*Pinguicula emarginata*), Orobanchaceae (*Pedicularis incisopetala*; Menzel et al. 1979), and Veronicaceae (*Microcarpaea*; Cook 1996; *Synthyris schizantha*; Hufford 1992, 1995). *Microcarpaea*, *Pedicularis incisopetala* and *Synthyris* are of special interest because their petals are not only lobed but also reduced in size; in some species of *Besseyia*, the sister of *Synthyris*, the corolla is tiny or almost lacking (*B. wyomingensis*) (Hufford 1995). Among Verbenaceae, petals are bilobed in some *Verbena* species. Also in Verbenaceae, the corolla tube has a ring of moniliform hairs at its entrance (e.g. *Verbena*, *Citharexylum*, *Ghinia*, *Petitita*).

An unusual feature are double petals with a dorsal and a ventral lobe in some *Columnnea* (Gesneriaceae) species (e.g. *C. incredibilis*; Kvist and Skog 1988; Weber 2004).

A spur or sac in the corolla tube has evolved here and there in several families, such as Gesneriaceae (e.g. *Drymonia*), Lamiaceae (*Plectranthus*), Lentibulariaceae (all genera), and Veronicaceae (e.g. *Antirrhinum*, *Linaria*). Two collateral spurs are present in the oil flowers of *Diascia* (Scrophulariaceae), and two collateral pouches in *Angelonia* (Veronicaceae) (Vogel 1974). These spurs, however, are a feature of the entire synorganized corolla (including the androecium), and not of single petals.

Asterids – euasterids I – Solanales

Among Solanales, only Convolvulaceae and Solanaceae have a few representatives with elaborate petals. In Convolvulaceae, some *Erycibe* species have lacinate petals (Hallier 1901). Bilobed petals are present in species of *Ipomoea* and *Argyreia*. Lobulate petals and, in addition, ventral petal scales are present in *Cuscuta* species (Liao et al. 2000; Derooin 2001); again, the petals are also reduced in size.

In Solanaceae, *Browallia* and *Salpiglossis* have bilobed petals; the strongly monosymmetric flowers of *Schizanthus* have petals with two and four lobes (Robyns 1931; Huber 1980).

Asterids – euasterids II – Bruniaceae

Bruniaceae commonly have petals with an inconspicuous peltate base (Leinfellner 1964) (Fig. 12G).

Asterids – euasterids II – Aquifoliales

In Cardiopteridaceae, *Citronella* has a prominent keel on the ventral side of the petals (Howard 1942; Karehed 2001). Less prominent keels are also present in a number of other former Icacinaceae (e.g. *Emmotum* group), which are now in Garryales (as Icacinaceae) (Karehed 2001). Otherwise, elaborate petals are not known from Aquifoliales.

Asterids – euasterids II – Apiales

In Apiaceae trilobed petals are common. The two lateral lobes are curved over the anthers in bud, the mid-lobe is prominently incurved and does not unfold at anthesis (von Gumpfenberg 1924); it may also attain various shapes (Froebe et al. 1982; Jahnke and Froebe 1984). Rarely, petals are flat and have 3–4 lobes (*Sinocarum schizopetalum*; Ying et al. 1993). In other families, elaborate petals have not been recorded.

Asterids – euasterids II – Asterales

The sister genera *Argophyllum* and *Corokia*, which constitute Argophyllaceae (Karehed et al. 1999), have broad-based petals with valvate aestivation. The petals have an appendage with many multicellular fringes at the base of the ventral side, which has been described as a ligule or corona (Fig. 12H–L) (Zemann 1907; Eyde 1966; Webb 1994) and may function as a nectar cover. In both *Argophyllum* and *Corokia* the ligule is devoid of vascular tissue (for *Corokia* see also Eyde 1966). In *Corokia* and perhaps also in *Argophyllum* the appendage covers the nectariferous disk at anthesis. In *A. cryptophlebium* the fringe surfaces have an irregularly papillate sculpture, while those of *C. cotoneaster* are smooth. However, it is not clear whether the fringes themselves are secretory.

Menyanthaceae and Goodeniaceae appear as well supported successive sister groups of Calyceraceae + Asteraceae (Lundberg and Bremer 2003). They share a unique kind of petal elaboration: their petals are induplicately valvate in bud (Endress 1975) and the petal part that is inside in bud is much thinner than the outer ones. The fold (induplicative area in bud) remains as a line in expanded petals (Gustafsson 1995). In some groups the two inner parts develop into two conspicuous lobes, whereas the primary petal apex remains as a minute tip between the lobes (*Nymphoides*, Menyanthaceae; *Dampiera*, *Velleia*, *Leschenaultia*, *Scaevola*, Goodeniaceae) (Carolin 1967; Holm 1988; Gustafsson 1995; Cook 1996). Petals with fringes on the margins are present in both families (e.g. *Nymphoides*; Cook 1996; *Velleia*; Carolin 1967). Fringes on the ventral surface are present in *Menyanthes* and in some species of *Nym-*

phoides (Cook 1996). In the water plant *Nymphoides* the fringes are water-repellent and prevent wetting of the inside of the flower (Armstrong 2002). Some *Nymphoides* have a tuft of plumose hairs on the petals close to the region of stamen insertion (Cook 1996; Erbar 1997). A corolline spur is present in species of *Anthotium*, *Goodenia*, and *Velleia* (Carolin 1959). Such a spur is also present in some Campanulaceae–Lobelioideae; all spur-bearing species are nested in the genus *Lobelia* (Koopman and Ayers 2005).

In *Stylidium* (Stylidiaceae) petals commonly have one, two or several ventral appendages at the entrance to the floral tube, which form a corona. In some species the petals are bilobed, in *S. calcaratum* trilobed (Erickson 1958).

Alseuosmia (Alseuosmiaceae) has the same unusual petal aestivation and shape of the unfolded petals as described above for Menyanthaceae and Goodeniaceae (Backlund and Donoghue 1996). Alseuosmiaceae may also have fringed (*Alseuosmia*) or crinkled petal margins (*Crispiloba*), and may have a ventral part that forms a corona (Lundberg and Bremer 2003).

In the large family Asteraceae there are no noteworthy specializations of the individual petals. Instead, evolutionary plasticity and elaboration is developed more at the level of the ensemble of the united petals, rather than at the level of individual petals.

Asterids – euasterids II – Dipsacales

The petals of Dipsacales are commonly simple. Those of *Scabiosa palaestina* (Dipsacaceae) are lobed (ternate) (Backlund and Donoghue 1996). In some Caprifoliaceae and Valerianaceae there are pouches or spurs with nectaries in the corolla tube (Wagenitz and Laing 1984; Hofmann and Göttmann 1990; Roels and Smets 1996).

Discussion

Among angiosperms, petals are a typical feature of eudicots. However, in basal angiosperms the use of the term ‘petal’ is problematic, because their perianth parts cannot be compared in every respect with those of eudicots (Hiepmo 1965; Endress 1994; Kramer et al. 2003). Nevertheless, a few exceptional cases do exist in basal angiosperms, in which the innermost perianth organs have particular elaborations that are comparable with petal elaborations of eudicots, such as, e.g. *Cabomba* (Cabombaceae, Nymphaeales) with nectariferous auricles at the base of the ‘petal’ blade (in addition, these ‘petals’ are retarded in development as are typical eudicot petals; Endress 2001), *Monodora* (Annonaceae, Magnoliales) with two lateral appendages of unknown function (Le Thomas 1969), *Artabotrys*

with a cucullate base, or other Annonaceae with food bodies or nectaries (Endress 1990), or also various Laurales with paired nectariferous appendages on staminodes (and stamens). In monocots there are many orchids with elaborate ‘petals’ (e.g. Vogel 2001); other families that include taxa with elaborate ‘petals’ are Iridaceae (*Patersonia*), Liliaceae (*Calochortus*), and Bromeliaceae.

In the basal grade of eudicots a first wave of petal differentiation occurred in Ranunculales (Kramer et al. 2003). In other basal eudicots petals and even sepals are sometimes not obviously differentiated, or they can be present or absent within families (Proteaceae; Douglas and Tucker 1996; Platanaceae; von Balthazar, pers. comm.; Trochodendrales; Endress 1986; Buxaceae and Didymelaceae; von Balthazar and Endress 2002a, b; von Balthazar et al. 2003). Still in some ‘basal’ core eudicots (i.e. small clades that are sister to the large, more diversified clades) this situation is unchanged (Gunnarales; Jäger-Zürn 1967; Soltis et al. 2003; Rutishauser et al. 2004; Saxifragales; Endress 1970, 1978, 1986, 1989a, b). The main evolutionary differentiation and elaboration occurred in the largest clades of eudicots, especially rosids.

Comparative structure

The simplest forms of lobed petals (or staminodes) are those with two or three lobes. If more lobes or subdivisions are present, usually a distinct middle lobe and several lateral lobes are discernible (Cunoniaceae p.p., Anisophylleaceae, Rhizophoraceae, Parnassiaceae, Saxifragaceae, Elaeocarpaceae, *Clarkia* and *Lopezia ciliatula* of Onagraceae). The middle lobe may either be the leading lobe (pinnate form) (Saxifragaceae) (Fig. 13A), or it may fit in with the lateral lobes in being secondarily lobed (ternate form) (Elaeocarpaceae) (Fig. 13C). More rarely, the petals have only lateral lobes (binate form) (most Caryophyllaceae with lobed petals, *Lopezia laciniata* of Onagraceae, Polygalaceae, Gillbeea of Cunoniaceae) (Fig. 13B). If there is a median lobe, it is sometimes not level with the lateral lobes but may be positioned more to the inside (Parnassiaceae) or more to the outside of the lateral lobes (especially in conduplicate petals) (Rhizophoraceae, Elaeocarpaceae). In other groups, the lobation appears more irregular in the mature stages (*Brexia* of Celastraceae, Corynocarpaceae, Malpighiaceae, Tropaeolaceae). Pinnate, ternate and binate forms develop by various metamorphoses of the median area of the petal, which is always leading development in the youngest stages. If lobation begins late, the shape will be pinnate, if it begins early, then the shape will be ternate or binate. If the flanks take the lead early on, the shape will be binate, if the median area and the flanks develop concurrently, the shape will be ternate

(von Gumpenberg 1924). Transitional forms between the three standard configurations also exist (Fig. 13D, E). In many families, petals with crinkled or undulate margins occur here and there, especially in large flowers, e.g. in Papaveraceae, Dilleniaceae, Lythraceae, caesalpinoid Fabaceae, Rosaceae, Hypericaceae, Malpighiaceae, Capparaceae, Cistaceae, Malvaceae, Ericaceae, Boraginaceae, Solanaceae, and Bignoniaceae. Whereas many simple petals of eudicots are conspicuously retarded in development up to late bud stages, it appears that elaborate petals do not tend to be retarded in bud. Instead, the lobes of divided petals may be incurved in bud, such as in Saxifragaceae (this study), Cucurbitaceae (this study), and in *Fuertesia* (Loasaceae) (Moody and Hufford 2000).

Peltate petals with ventral lobes are known from many families; sometimes the lobes are ligule-like (forming a broad horizontal scale), sometimes they are combined with a more or less cucullate petal base, and then the petals are not clearly peltate (i.e. not with a unifacial base). If the ventral lobes are present at the entrance of a floral tube, then they may form a corona or paracorolla. Ventral elaborations are common in some families, such as Ranunculaceae, Caryophyllaceae (Caryophyllaceae), Erythroxylaceae, Tropaeolaceae, Resedaceae, Sapindaceae, and rare in others, e.g. *Reaumuria* (Tamaricaceae), *Waldsteinia* (Rosaceae), *Cleome* (Cleomaceae), *Nemophila* and other Boraginaceae (Baum 1950; Hiepko 1965; Rohweder 1967; Guédès 1968; Ronse De Craene 1990; Kosuge 1994; Erbar et al. 1998). In many Boraginoideae they are hollow scales (Arber 1939). The ligules may also be divided, either tangentially (*Argophyllum* and *Corokia* of Argophyllaceae, *Lophopetalum* and *Solenospermum* of Celastraceae) or radially (*Erythroxylum* of Erythroxylaceae, many Sapindaceae).

Morphological interpretation of divided petals and staminodes

The morphological interpretation of ligules and corona (paracorolla) elements is not always clear. These structures are situated between the petal and stamen whorl. If they form scales on the ventral surface of the petals, they are commonly interpreted as parts of the petals (e.g. Erythroxylaceae, Sapindaceae; Leinfellner 1954a, 1958). However, if they are fused with the petals only at the very base (but still in the same radius, e.g. *Parnassia*), or if they form one or more separate series of parts (e.g. Passifloraceae), their interpretation becomes more difficult. They may then be classified as staminodes (as commonly interpreted in *Parnassia*), as novel formations (as interpreted in Passifloraceae, Bernhard 1999), or still as elaborations of the petals.

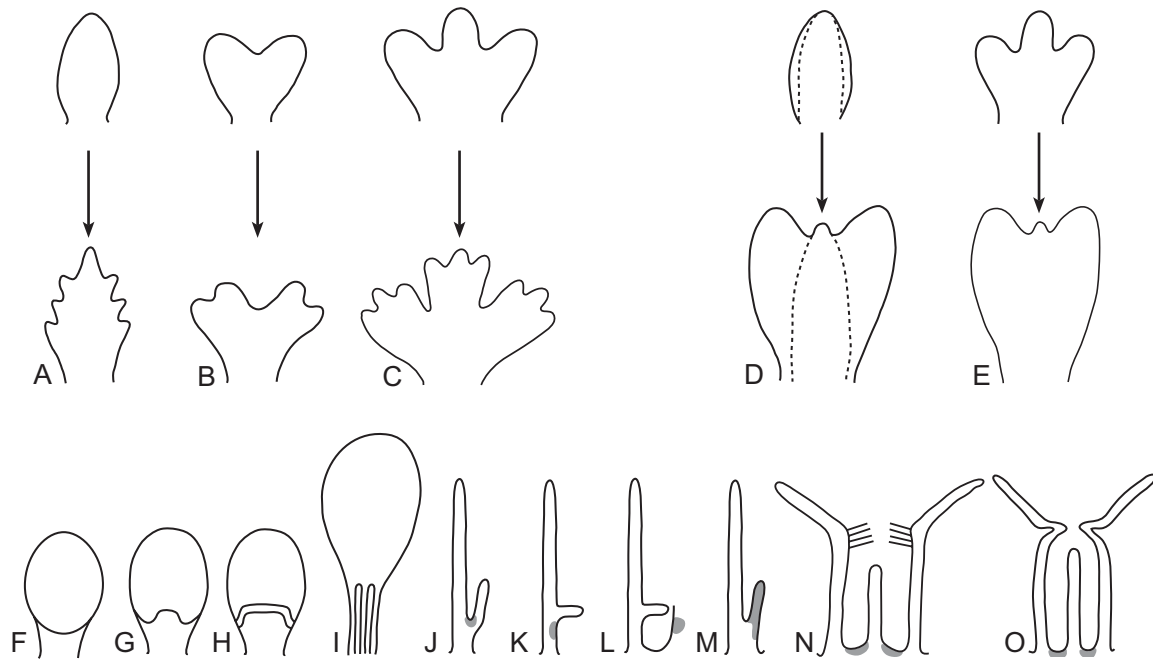


Fig. 13. Shape and development of elaborate petals; schematic representation of recurrent forms. (A–E) Development of marginal lobes; (A) from simple to pinnate; (B) from bilobed to doubly bilobed (binate); (C) from trilobed to doubly trilobed (ternate); (D) simple early stage and overtopping of primary apex by two lateral lobes; (E) trilobed early stage and cessation of development of primary apex. (F–G) Petal with ventral lobe. (H) Petal with two ventral lobes. (I) Petal with two longitudinal ridges on claw. (J–M) Petals with ventral lobe associated with nectaries (gray), in longitudinal section, ventral on the right; (J) nectary in pouch; (K) nectary below ventral lobe; (L) nectary not on petal but topographically associated with ventral lobe; (M) entire ventral lobe nectariferous. (N–O) Salverform flowers in longitudinal section; (N) floral entrance covered by ring of hairs; (O) floral entrance constricted by hollow scales.

Developmental and molecular genetic studies may then be required for better resolution.

The ‘ligule’ in *Corokia* was interpreted as part of the petal (Eyde 1966), in *Argophyllum* as a staminode (Zemann 1907). However, in view of the close relationship between the two genera these structures are most likely homologous. These ‘ligules’ have similar shapes in both genera and are devoid of vasculature (for *Corokia*; Eyde 1966; *Argophyllum*; this study). In contrast, in Erythroxylaceae (Leinfellner 1954a) and Sapindaceae (Radlkofer 1896; Leinfellner 1958) the ligule is vascularized.

The sheathing corona of *Pachynema* (Dilleniaceae) is perhaps derived from staminodes (Craven and Dunlop 1992). This interpretation is plausible because in Dilleniaceae the stamens are initiated centrifugally, and in *Dillenia* the last initiated, outermost organs are then often reduced and represent staminodes without being further elaborated (Endress 1997); moreover, in *Schumacheria* the stamens are basally united (Craven and Dunlop 1992). The interpretation of the corona in Malpighiales (Passifloraceae, Malesherbiaceae, Turneraceae, Ochnaceae) is more puzzling. Puri (1948) interpreted the inner series of the corona of *Passiflora* as staminodial, the outer series as ventral elaborations of sepals and petals.

Another possibility is that the corona neither consists of staminodes nor ventral parts of petals but instead represents a new formation, as the structural elements are not directly associated with the individual petals plus the androecia are not polystemonous (apart from a few Ochnaceae) (Bernhard 1999).

For an evaluation of these questions, comparative ontogenetic investigations would be required, which are beyond the scope of the present study. It may be expected that the morphological basis for divided petals and staminodes is diverse, and also that complex structures may be based on single organs or on a complex of several united organs. The clearest case for a structure composed of several organs are the cucullate, appendaged corona elements in Loasoideae (Loasaceae). They are interpreted as consisting of three united staminodes, as suggested by their development (Leins and Winhard 1973; Hufford 1990, 2003).

Ventral elaborations on petals, such as paired mounds in Ranunculaceae and paired corona scales in Caryophyllaceae, were interpreted by Erbar et al. (1998) and Leins et al. (2001) as homologous to ventral pollen sacs of stamens. This will be interesting to study from a molecular developmental point of view.

Morphology and architecture

The organs of a flower are synorganized into a more or less complicated architecture, in which functional parts may consist of different structural elements. In sympetalous flowers or in salverform choripectalous flowers petal elaborations often transcend single petals and are rather expressed in the context of the entire corolla architecture. Sprengel (1793) and Delpino (1870) noted early on that there is a trend to protect the nectary and pollination organs by corolla elaborations.

Petals with a valvate estivation in bud may develop appendages outside and/or inside the bud close to the contiguous area (e.g. in Myrtaceae and Rubiaceae) (Drinnan and Ladiges 1988; Robbrecht 1988).

A hair ring is often present at the entrance of the tube of salverform flowers (e.g. Olacaceae, Loganiaceae, Rubiaceae, Verbenaceae, *Zaluzianskya*, Scrophulariaceae) (Fig. 13N). Hollow scales that constrict the width of the entrance are present in Boraginaceae and, perhaps, *Androsace* (Primulaceae) (Arber 1939) (Fig. 13O).

Another method of closure of the floral entrance is by an upward arching of the lower lip (formed by three petals), which is elastically opened by pollinators. This architecture ('personate' flowers), is known from genera of several families of Lamiales: Acanthaceae (*Linariantha*), Bignoniaceae (*Amphilophium*, *Stereospermum*), Lentibulariaceae (*Utricularia*), Gesneriaceae (*Didymocarpus*), and Veronicaceae (*Antirrhinum*, *Linaria*) (see Endress 1994).

In the formation of a spur in sympetalous taxa, more than one petal may also be involved, such as in Veronicaceae (*Antirrhinum*, *Linaria*), Lamiaceae (*Plectranthus*), Campanulaceae (*Lobelia*), and Goodeniaceae (*Goodenia*, *Velleia*) (Carolin 1959; Endress 1994). Spurs are commonly nectar holders but may also serve to stabilize floral architecture in some of these cases (see below).

In some Acanthaceae the upper lip of the corolla forms two longitudinal ridges on the ventral side, which support the thin style. This apparatus is formed by synorganization of the two upper petals (Troll 1951; Schönenberger 1999).

Comparative potential function of petal elaborations

Elaborate petals and staminodes have assumed a diversity of functions in different groups. However, in most cases detailed studies are lacking. Based on our current knowledge a number of potential functions are discussed below.

(1) *Nectar production* (Fig. 13J, K, M): Petals bear nectaries in many 'core' Ranunculales (Ranunculaceae, Berberidaceae, Lardizabalaceae, Menispermaceae). The

petals are either small and simple, with their nectaries exposed (e.g. *Xanthorrhiza*, *Caulophyllum*, *Sinofranchetia*, *Menispermum*), or they are larger with nectaries in basal pockets (e.g. *Ranunculus*, *Nigella*) or spurs (e.g. *Aquilegia*, *Delphinium*, *Epimedium*) (e.g. Hiepko 1965; Kosuge 1994; Tamura 1995; Erbar et al. 1998). In other groups, nectariferous petals are more rare. In *Ryparosa* (Achariaceae) the basal ventral scale of the petals is a nectary and bears hairs that cover the nectariferous surface (this study). In Corynocarpaceae the alternipetalous staminodes are similar (but without hairs) (Matthews and Endress 2004) (see also below). In *Dirachma* (Dirachmaceae) the nectary is situated at the petal base below, and covered by, a ventral protrusion (Link 1991, 1994; Ronse De Craene and Miller 2004). In *Grewia* (Malvaceae) the nectary is in the cucullate base of the petal (Vogel 2000). In Swertiinae (Gentianaceae) nectaries are in pairs at the petal base and are often covered by fringes, in *Halenia* they are hidden in spurs (von Hagen and Kadereit 2001). Nectary disks in some families consist of several portions (that may be derived from staminodes). Rarely, these portions may again be subdivided into several lobes. This is present in *Helictonema* (Celastraceae) (Robson et al. 1994), *Lophopetalum* spec. (Celastraceae) (Loesener 1942), *Brexia madagascariensis* (Celastraceae) (Matthews and Endress 2005b), *Greyia flanaganii* (Greyiaceae) (Vogel 1954), and *Spiranthera odoratissima* (Rutaceae) (Engler 1926). There is a general evolutionary tendency of nectaries to become lobed in flowers with high nectar production (see, e.g., Endress 1994).

(2) *Nectar cover* (Fig. 13J–L, N, O): Basal ligules or cuculli or pocket-like structures may have a function as nectar covers to protect against nectar thieves or prevent nectar dilution or evaporation. This has been mentioned for *Corokia* (Eyde 1966; Webb 1994), and may also be true for *Argophyllum* (both Argophyllaceae). In *Erythroxyton* (Erythroxyllaceae) (Leinfellner 1954a) and many Sapindaceae (Radlkofer 1896; Leinfellner 1958) the ventral part of the double ligule has the same function. In *Crossostylis* (Rhizophoraceae) fringed lobes in the floral center that are not clearly associated with outer organs cover the nectaries (Juncosa 1988). In *Carallia*, *Gynotroches* and *Pellacalyx* (Rhizophoraceae), where the flowers are not widely gaping and the petal appendages remain incurved at anthesis, the petal appendages may have a similar effect. The carpet of multicellular outgrowths on the ventral side of the petals ('tepals') of *Thesium* species (Santalaceae) may also have this function. The 'staminodes' of *Corynocarpus* (Corynocarpaceae) that bear a basal nectary (see above) have a thin and broad upper part with an apparent nectar cover function (Matthews and Endress 2004). In most of these examples, the nectaries are located on a disc toward the floral center, in front of the petals. More

rarely, such petal appendages cover nectaries that are located on the petals themselves (see above).

(3) *Nectar holder*: Spurs that produce nectar also function as nectar holders (Hodges 1997; Kadereit and von Hagen 2003). Rarely, petals (or staminodes) produce pockets or spurs that do not produce nectar but only serve as nectar holders, the nectar being produced by neighboring organs. In Fumarioideae (Papaveraceae) and *Viola* (Violaceae), nectar is produced at the base of the stamens, in *Linaria* (Veronicaceae) it is produced on a disk at the base of the gynoecium and may reach the tip of the spur by a capillary duct (Vogel 1998). In Loasaceae, the concave (cucullate) staminodial groups may serve as nectar holders, while the nectar is produced at the base of the gynoecium (Brown and Kaul 1981; Hufford 1990; Weigend et al. 2003, 2004; M. Weigend, pers. comm.).

(4) *Pseudonectaries*: In some *Parnassia* species the thickened ends of the finger-like staminodial lobes have the function of pseudonectaries serving as optical attractants mainly for certain Diptera (Sandvik and Totland 2003, and literature cited therein). They act with their smooth surface alone and do not show any secretion. In *Gillbeea*, the same function has been surmised (Endress 1994). However, the glistening effect in *Gillbeea* is attained by a cover of an (oily) secretion (Endress 1994). In *Parnassia palustris* the nectaries are on both sides of the median finger, which is located on the ventral surface of the staminode (Daumann 1932).

(5) *Water storage*: For mangrove taxa of Rhizophoraceae (*Bruguiera* and *Ceriops*) with diurnal flowers (not for those with nocturnal flowers) it was found that the thickened ends are filled with trache(o)ids; consequently, the latter were interpreted as water storage organs (Juncosa and Tomlinson 1987, 1989b). Tobe and Raven (1988) also observed thickened appendage tips full of tracheoids in *Anisophyllea* and *Poga* (Anisophylleaceae); these may have a similar function. In both Rhizophoraceae and Anisophylleaceae, petals with thickened appendage ends are accompanied by valvate estivation of the sepals, which provides efficient protection in bud due to the cohesion along their flanks in bud. A possible function of the thickened petal appendage ends could be to assist opening of floral buds by turgidity.

(6) *Non-nectarial secretion*: In the families with the most elaborate divided petals the repeated occurrence of appendages with thickened ends is striking, e.g. in Anisophylleaceae, Cunoniaceae, Parnassiaceae (staminodes), Malpighiaceae, and Rhizophoraceae. The thickening could suggest a secretory activity for these parts. They were described as glands in those Anisophylleaceae in which they occur (e.g. Tobe and Raven 1988). Among Rhizophoraceae, the appendages are slightly thickened at the end in *Bruguiera*, *Ceriops*, and *Pellacalyx*, and hydathodes are present (Juncosa and Tomlinson 1987). In *Bruguiera gymnorhiza*, where living flowers could be

examined under the stereomicroscope, no traces of secretion were found on the appendages. In the material studied by SEM, remains of secretions on petals were present in buds of *Rhizophora* cf. *mucronata* and *Ceriops*. However, there is no evidence for its origin from the appendages. The only genus in which secretion was found on the thickened ends was *Gillbeea* (Cunoniaceae) (Endress 1994) (see above).

(7) *Secondary pollen presentation*: In *Hypocoum* (Papaveraceae) the middle lobe of the petals is involved in secondary pollen presentation. It either takes up pollen from one and two half anthers, folds up, and then gives off pollen in portions (*H. leptocarpum*) (Yeo 1993), or the petal lobe is first appressed to the anthers and then slowly rolls back and downwards from the apex, thus presenting only few pollen grains at a time (*H. procumbens*) (Dahl 1989). Although the anthers open already in bud, giving off the pollen into the middle lobe of the two inner petals, the flowers are functionally protogynous, with the stigma receptive before pollen is openly presented on the petals (Dahl 1989). In *Acrotriche* (Ericaceae) petals bear hairy tufts that act as pollen presenters (McConchie et al. 1986).

(8) *Pollen application to pollinators*: In representatives of Elaeocarpaceae (incl. Tremandraceae) and Rhizophoraceae the petal flanks are curved inwards (induplicative-valvate in Elaeocarpaceae, conduplicate in Rhizophoraceae). In taxa of both families each petal embraces several stamens (Rao 1953; Juncosa 1988; Matthews and Endress 2002), but functions are different. In Elaeocarpaceae (incl. Tremandraceae) this is a mechanism to assist in buzz-pollination by bees. The folded petals form a guiding device to direct the pollen shooting out of the anthers. An analogous petal function – though in entire flowers in which the ensemble of all petals is connivent and the individual petals are not elaborate – occurs in Ochnaceae (Kubitzki and Amaral 1991). In contrast, in Rhizophoraceae this architecture is the basis of an explosive mechanism: it has been suggested that touching the distal petal parts in some Rhizophoraceae may trigger the explosive opening of the petals (*Ceriops tagal*; Tomlinson et al. 1979). However, in other species sensitive hairs towards the base of the petals have this function (*Bruguiera sexangula*; Gehrmann 1911; Tomlinson et al. 1979; Yeo 1993; *B. exaristata*; Tomlinson et al. 1979). This explosive mechanism requires the action of birds or strong insects. In *Ceriops* pollination is by moths (Tomlinson et al. 1979). In *Bruguiera eriopetala* birds or bees may trigger the petals and receive a shower of pollen on their body (Davey 1975; Tomlinson et al. 1979; Kondo et al. 1987, 1991; Tanaka 1989; Noske 1993).

(9) *Optical nectar guide*: Petal appendages (corona, paracorolla) that are situated near the entrance to the nectar source may exhibit a color, especially yellow, that

contrasts with that of the other floral parts, thus functioning as nectar guides. This is the case in *Cardiospermum* (Sapindaceae) and *Polygala* (Polygalaceae), and Caryophylloideae (Caryophyllaceae). Similarly, the staminodial scales of Loasoideae function as optical nectar guides. We are unaware that the corona (paracorolla) in *Pachynema* (Dilleniaceae) (Craven and Dunlop 1992), *Lophopetalum* and *Solenospermum* (Celastraceae) and *Erythroxylum* (Erythroxylaceae) also exhibits contrasting colors. In *Stephanodaphne* (Thymelaeaceae), the floral tube terminates with a ring of numerous irregular protuberances (forming an “annulus”) (Rogers 2004); the morphological nature of these protuberances is unclear. In Polygalaceae the appendage of the keel either develops a color contrasting with the other floral parts (*Polygala*; Heubl 1984), or it forms the main optically attractive part of the flower (*Muraltia*; pers. obs.).

(10) *Mechanical nectar guide* (Fig. 13I): Petals of salverform flowers may have longitudinal ridges on their claws, which act as guiding structures to the nectary, as in *Silene* (Caryophyllaceae) (Rohweder 1967), *Geranium robertianum* (Geraniaceae) (pers. obs.), and *Phacelia* (Boraginaceae) (Brand 1913).

(11) *Optical enhancement of floral periphery in night-pollinated flowers*: Vogel (1954) has pointed out that subdivision of the petal contours, together with a light color, enhances visibility of the flowers to nocturnal pollinators, especially sphingids. Earlier, Delpino (1870) mentioned that fimbriae increase optical attraction. Such subdivisions are present in, for example, some species of *Pelargonium* (Geraniaceae), *Dicranolepis* (Thymelaeaceae), *Impatiens* (Balsaminaceae) (Vogel 1954), a number of Caryophyllaceae (especially *Dianthus* and *Silene*), *Lithophragma* (Thompson and Pellmyr 1992), and in *Viola cazorlensis* (Herrera 1993). In this category the flowers of *Cassipourea* (Rhizophoraceae) with their plumose petal appendages should also be mentioned (Juncosa and Tomlinson 1989a). In *Zaluzianskya* (Scrophulariaceae) it appears that the petals are more deeply bilobed in the night-flowering species than in the diurnal ones (Hilliard 1994).

(12) *Flickering bodies for attraction of flies*: Mobile appendages of various kinds are present in some highly elaborate fly pollinated flowers, among eudicots with a peak in petals and coronas of asclepiadoid Apocynaceae (Vogel 2001).

(13) *Landing platform for pollinators*: In some Polygalaceae the divided appendage on the keel petal functions as a landing platform for pollinating bees (Heubl 1984). In *Mitella* (Saxifragaceae), single linear pinnae of the pinnate petals act as footholds for pollinating fungus gnats; the latter hold on to the thin structures with spurs on their legs (Okuyama et al. 2004). In the closely related *Tolmiea* the petals are linear, thread-like, and have the same function

(Goldblatt et al. 2004). The corona scales in some asclepiadoid Apocynaceae may also function as footholds for pollinators (Vogel 1961). The footholds on the convex lower lips of flowers in which the nectar has to be reached by using some force may also have an elaborate surface sculpture with notches or ribs (e.g. Faboideae; Stirton 1981; *Linaria*; Müller 1929; *Thunbergia*; Endress 1994).

(14) *Reinforcement of architecture* (Fig. 13I): Free petals with elongate claws in salverform flowers may have two longitudinal ridges that provide firmer architecture, as in some Caryophylloideae (Caryophyllaceae) (Rohweder 1967) and *Geranium robertianum* (Geraniaceae) (pers. obs.). In addition, these ridges, together with the other organs in the tubular part of the salverform architecture, may also function as guides for the probosces of pollinators (see above). In Faboideae (Fabaceae), the hooks of the wing petals and the ventral protrusion on the flag petal may serve as a reinforcement of the keel flower architecture. Also on flat flowers, the petals may have longitudinal ribs that may have a function in reinforcement of the floral platform; in this case the petals are somewhat convexly bent (*Mangifera*, Anacardiaceae; *Maytenus*, Celastraceae; Matthews and Endress 2005b). A reinforcement may also be provided by bulged-out or bulged-in parts of sympetalous corollas, such as spurs or the convex lower lip in personate flowers (Burt 1964; Endress 1994).

(15) *Stylar support*: In some Acanthaceae the median upper part of the corolla forms two longitudinal rims, or a fold on the ventral side, which provides support to the thin style and holds it in the median plane (Troll 1951; Schönenberger 1999).

(16) *Prevention of dunking and wetting of flowers in water plants*: In the water plant *Nymphoides* (Menyanthaceae) fringes on the margins of the petals prevent the submerging of flowers because of surface tension (Armstrong 2002) created by the fringes. Fringes on the ventral surface of the petals may be water-repellent and prevent wetting of the upper side of the flower. In some *Utricularia* species (Lentibulariaceae) the closure of the flower by the convex lower lip has the same function (Jérémie 1989).

(17) *Fleshy part of drupe-like fruits*: In *Coriaria* (Coriariaceae) the petals attain their main function only in fruit. They become fleshy and form the outer, fleshy layer of the drupe-like fruits, in which the carpels functionally constitute the pyrene (Matthews and Endress 2004; pers. obs.).

Evolutionary trends, correlations

During the compilation of data for this study it became obvious that often families exhibiting a tendency towards petal diminution (small, narrow, acute petals) or even

petal loss also contained taxa with marginally subdivided, lobed petals. Thus, it appears that petal lobation and petal reduction are somehow evolutionarily connected. The association was found in Caryophyllaceae, Hamamelidaceae, Rhamnaceae, Saxifragaceae, Cunoniaceae, Anisophylleaceae, Cucurbitaceae, Euphorbiaceae, Rhizophoraceae, Resedaceae, and Thymelaeaceae. In the Rhynochocalycaceae/Penaeeae group, petals are lobed in the former, and lacking in the latter (Schönenberger and Conti 2003). There may be parallel petal reduction series within a single genus or even species. *Rotala fimbriata* (Lythraceae) has fimbriate petals, while some other species of *Rotala* are apetalous (Koehne 1903; Cook 1996). In *Sloanea* (Elaeocarpaceae) some species are apetalous, and in the petaliferous species the petals are lobed (Coode 2004). In *Ceratopetalum* (Cunoniaceae) petals are lobed, and one species is apetalous (Bradford et al. 2004). *Combretocarpus rotundatus* (Anisophylleaceae) has either lobed, filamentous petals or is apetalous (Matthews et al. 2001; this study). In *Adenia* (Passifloraceae) small, narrow petals and fringed petals are present (Harms 1925b). In the *Synthyris-Besseyia* group (Veronicaceae), *Synthyris schizantha* has lacerate petals, and in *Besseyia* the petals are reduced (Hufford 1992, 1995). In *Hilsenbergia* (Boraginaceae), *H. schatziana* has lobulate petals, whereas *H. apetala* technically lacks petals (although the petal tube still holds the stamens together, but the petals do not have an extension beyond the level of stamen attachment) (Miller 2003). The petals in *Cuscuta* are reduced (small) compared to other Convolvulaceae, and they may also be lobulate. In *Pedicularis incisopetala* (Orobanchaceae) the petals are incised and reduced (Menzel et al. 1979).

In salverform flowers there is a tendency towards convergent, parallel variation in the formation of bilobed petals and denticulate petals in the same families (Caryophyllaceae, Primulaceae, and Polemoniaceae).

Subdivided petals tend to be associated with sepals that have a valvate estivation and are postgenitally coherent in bud (e.g. Myrtales, Anisophylleaceae, Cunoniaceae, Elaeocarpaceae, Celastraceae, Rhizophoraceae).

In Grewioideae there is an interesting evolutionary plasticity in the position of the nectary. In some groups (e.g. *Grewia*) the nectary is located on the petal, in others it is slightly displaced to the androgynophore (e.g. *Corchorus*). Thus the nectary transgresses morphological boundaries but still remains in the same topographical area.

In some Rhizophoraceae, the pinnae may be distinct only in the first stages of development, and thus the petals appear entire at maturity, e.g. in *Crossostylis* (Juncosa and Tomlinson 1989b) and *Rhizophora*. In *Rhizophora × lamarckii*, the mature petals have three tips that may correspond to the longer appendages in

other Rhizophoraceae. Thus these tips may represent reduced lobes. It appears that these seemingly unlobed petals of *Crossostylis* and *Rhizophora* are evolutionarily derived from lobed petals (Fig. 14E).

Lobed petals occasionally occur in single mutants among families with otherwise simple petals (see also Mabberley and Hay 1994).

Systematic aspects

Subdivided or otherwise elaborate petals are not common but are present here and there in many families and orders of core eudicots. They are least common in basal eudicots, for which there may be two reasons: the flowers are in general less elaborate than those of core eudicots, and many basal eudicots do not have petals at all. This raises the questions, whether there are larger clades in which elaborate petals are more concentrated than in others, and whether certain kinds of elaborations may be used to support disputed relationships between groups.

(1) Core Ranunculales, which form a clade (Hoot and Crane 1995), share nectariferous petals. In simple forms nectar is openly presented. Such petals occur in all four families, either predominant (Menispermaceae) or rare (Berberidaceae, Lardizabalaceae, Ranunculaceae). These flowers all have a fly pollination syndrome (Endress 1995). In the latter three families, genera with such petals tend to be phylogenetically basal; it should be further explored whether this petal form is ancestral in the core Ranunculales. Petals with ventral elaborations forming nectar pockets occur in Ranunculaceae and Berberidaceae, petals with marginal elaborations only in a few Ranunculaceae.

(2) Petals with ventral scales are present among Caryophyllales in the sister families Frankeniaceae (Leinfellner 1965) and Tamaricaceae (*Reaumuria*) (Ronse De Craene 1990; Gaskin 2002).

(3) Anisophylleaceae and Cunoniaceae share strikingly similar flower forms (Figs. 5A, 10C) (Matthews et al. 2001; Schönenberger et al. 2001). One of several shared features is hand-shaped petals. However, in molecular analyses the two families appear in separate orders, Oxalidales and Cucurbitales, which themselves appear not to be closely related (Schwarzbach and Ricklefs 2000; Soltis et al. 2000; Savolainen et al. 2000; APG 2003; Zhang et al., 2006). Nevertheless, after a comparative study of the floral structure of all families of these two orders, the flowers of Anisophylleaceae still appear to be more similar to those of Cunoniaceae than to those of any family of the Cucurbitales (Matthews and Endress 2002, 2004). Molecular phylogenetic studies with more genes on a broader sample of core eudicots are still needed to tackle the poorly supported relationships between many of the orders of rosids.

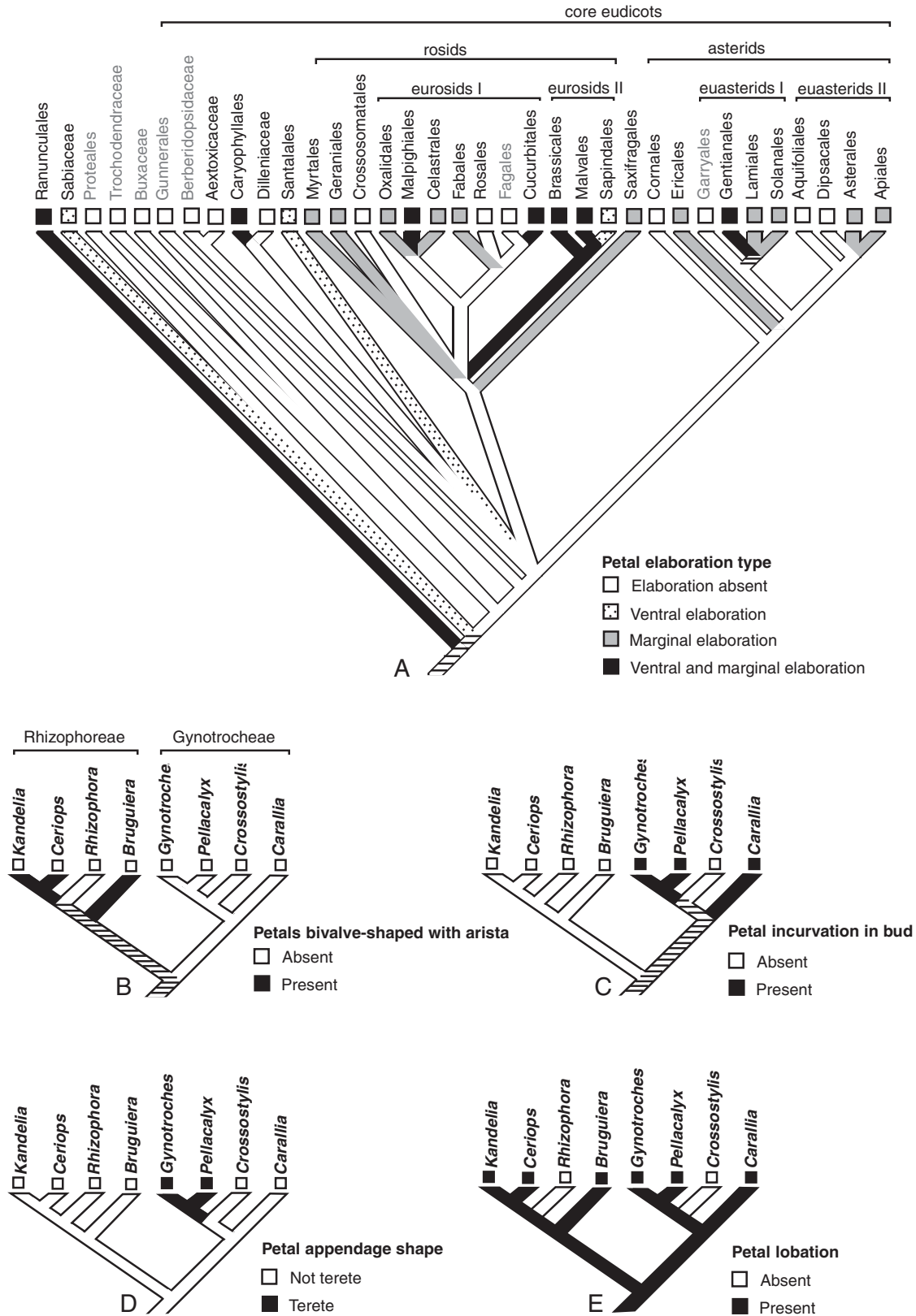


Fig. 14. Distribution of petal features in cladograms (MacClade 4.0). (A) Eudicots; names of orders without petals printed in gray (topology from APG 2003); features scored as present only if found to occur in more than one genus of an order. (B–E) Rhizophoraceae (tribes Gynotrocheae and Rhizophoreae) (topology from Schwarzbach and Ricklefs 2000).

(4) Cunoniaceae and Elaeocarpaceae appear as well supported sisters to each other in the 3-gene analysis by Soltis et al. (2000). Both have petaliferous and apetalous representatives, and in both families a good portion of the petaliferous ones have subdivided petals with a middle lobe and two (or more) lateral lobes (ternate form). It may be assumed that the propensity to form this kind of subdivided petals (or to lose petals) is a synapomorphy for this clade.

(5) The position of Parnassiaceae as sister to Celastraceae, or nested in a basal clade of Celastraceae, based on molecular studies (Soltis et al. 2000; Simmons et al. 2001; Simmons 2004a, b; Zhang and Simmons, 2006), is supported by the shared presence of fimbriate petals (pinnate form) (*Salacighia*, *Lophopetalum*, *Parnassia*), and by the shared presence of subdivided staminodes or nectary lobes (*Brexia*, *Helictonema*, *Lophopetalum*, *Parnassia*) (Matthews and Endress 2005b).

(6) The presence of a corona in Passifloraceae, Malesherbiaceae, and Turneraceae (Malpighiales) supports the close relationships of these families, which are supported also by other floral similarities and by molecular studies (Savolainen et al. 2000; Chase et al. 2002). In addition, a number of Malpighiales have ventral petal lobes (Achariaceae, Turneraceae, Hypericaceae, Linaceae, Erythroxylaceae). However, the relationships among most families of Malpighiales are not yet established (Savolainen et al. 2000; Chase et al. 2002; Gustafsson et al. 2002; Davis et al., 2005).

(7) In Celastrales, Malpighiales, and Oxalidales (these three orders forming a weakly supported clade; Savolainen et al. 2000), similarities in petals, such as the relatively frequent occurrence of fringed margins, could represent homoplastic tendencies that are based on certain shared genetic preconditions (Matthews and Endress 2002, 2005b).

(8) Two clades (tribes) within Rhizophoraceae are supported by special petal elaborations (Fig. 14B–E): Rhizophoreae have bivalve-shaped petals with an arista (Fig. 14B), Gynotrocheae have petals incurved in bud (Fig. 14C). The sister pair *Gynotroches* and *Pellacalyx* has terete petal appendages (Fig. 14D).

(9) A number of Brassicales are characterized by ventral petal scales and/or cucullate petal bases (Cleomaceae p.p., Emblingiaceae, Pentadiplandraceae, Resedaceae, Tropaeolaceae). However, they do not seem to be especially closely related within Brassicales (Savolainen et al. 2000).

(10) Eurosids II are characterized by relatively many clades with ventral petal elaborations (Fig. 14A).

(11) The position of *Corokia* together with *Argophyllum* in a clade (Argophyllaceae), based on *rbcL* and *ndhF* (Karehed et al. 1999), is supported by the presence of similar multifid petal ligules in *Argophyllum* and *Corokia* (see also Hallier 1908; Engler 1930a; Eyde 1966; Takhtajan 1997). Such multifid petal ligules are not

present in other genera of the earlier Escalloniaceae s.l., into which *Corokia* and *Argophyllaceae* were formerly placed (Engler 1930a).

(12) The relationship of Menyanthaceae and Goodeniaceae as successive sister groups of Calyceraceae + Asteraceae (Lundberg and Bremer 2003) is supported by a shared type of petal elaboration based on induplicative-valvate petal estivation. This type is also present in Alseuosmiaceae, which are also in Asterales but are more distantly related with Menyanthaceae and Goodeniaceae.

Outlook

This study is an attempt to deal with the diversity of petals in eudicots. We concentrate on extreme formations across the spectrum of possibilities. Other dimensions that should be explored are patterns of development and patterns of histology across the eudicots. For instance: How common is developmental retardation of petals? What is the relationship between sepal aestivation and such petal retardation? What is the relationship between sepal aestivation and histological differentiation of petals? How common is participation of petals in the floral envelope, and at what systematic level is it variable? How should petals be defined? How many times did petals originate in angiosperms? A broad range of approaches between systematics and molecular developmental genetics should lead to further progress.

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