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Extrafloral nectaries in Leguminosae: phylogenetic distribution, morphological diversity and evolution

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Abstract. Extrafloral nectaries (EFNs) mediating ecologically important ant–plant protection mutualisms are especially common and unusually diverse in the Leguminosae. We present the first comprehensively curated list of legume genera with EFNs, detailing and illustrating their systematic and phylogenetic distributions, locations on the plant, morphology and anatomy, on the basis of a unified classification of EFN categories and a time-calibrated phylogeny, incorporating 710 of the 768 genera. This new synthesis, the first since Mckey (1989)'s seminal paper, increases the number of genera with EFNs to 153 (20% of legumes), distributed across subfamilies Cercidoideae (1), Detarioideae (19), Caesalpinioideae (87) and Papilionoideae (46). EFNs occur at nine locations, and are most prevalent on vegetative plant parts, especially leaves (74%) and inflorescence axes (26%). Four main categories (with eight subcategories) are recognised and include the following: formless, trichomatic (exposed, hollow), parenchymatic (embedded, pit, flat, elevated) and abscission zone EFNs (non-differentiated, swollen scars). Phylogenetic reconstruction of EFNs suggests independent evolutionary trajectories of different EFN types, with elevated EFNs restricted almost exclusively to Caesalpinioideae (where they underwent spectacular morphological disparification), flat EFNs in Detarioideae, swollen scar EFNs in Papilionoideae, and Cercidoideae is the only subfamily bearing intrastipular EFNs. We discuss the complex evolutionary history of EFNs and highlight future research directions.

Additional keywords: ant–plant interactions, extranuptial nectaries, Fabaceae, mutualism, nectar, plant defense, legume phylogeny.

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Introduction

Extrafloral nectaries (EFNs) mediate the most widespread and ecologically important indirect plant mutualistic defence mechanism against herbivores (Heil 2015). EFNs secrete a carbohydrate-rich nectar reward to attract especially ants, but also other aggressive arthropods, and exploit and rely on them as 'bodyguards' (Bentley 1977; Kessler and Heil 2011). These ecologically important ant–plant mutualisms involving EFNs have evolved many times independently in over 100 angiosperm families and some ferns (Weber and Keeler 2013) and are hypothesised to have spurred plant diversification (Weber and Agrawal 2014). EFNs are particularly common in the legume family, Leguminosae (=Fabaceae), the third largest angiosperm family, which is well known for its rich diversity of interactions with ants (Mckey 1989), including textbook examples such as ant 'acacias' and their obligate aggressive ant mutualists, which are critical to enhance plant competitive ability and survival (Janzen 1966).

Extrafloral nectaries in legumes have been known since even before the term 'extrafloral' nectary had been coined, with reports of nectar-secreting *glandulae* (lit. glands) on leaves in the genera, *Bauhinia*, *Cassia s.l.*, and *Mimosa* (Hall 1762[1]). Yet, it took nearly 200 years to gradually assemble a more complete understanding of EFNs in this family, culminating in Mckey's (1989) seminal paper, which provided the most recent comprehensive review of EFNs and their associated

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[1] Also published in Carl von Linné's *Amoenitates academica*, vol 6. *Laurentius salvius* (pp. 263–278).

interactions in legumes. Since then, there has been much renewed interest in exploring aspects of EFN diversity, ecology and evolution in and beyond legumes (see Marazzi *et al*. 2013*a*) and, equally importantly, the taxonomy of the family has undergone substantial realignments in terms of generic delimitation, and the tribal and subfamily classification, largely as a result of insights from molecular phylogenies (see Lewis *et al*. 2005; Legume Phylogeny Working Group 2013, 2017). Recent collaborative work by the Legume Phylogeny Working Group (LPWG) resulted in a community-endorsed revised subfamily classification of the family, recognising the following six robustly supported monophyletic subfamilies (Legume Phylogeny Working Group 2017): (1) the re-circumscribed Caesalpinioideae DC. (including the former subfamily Mimosoideae now referred to informally as the mimosoid clade), (2) Cercidoideae LPWG (revised circumscription), (3) Detarioideae Burmeist., (4) Dialioideae LPWG (revised circumscription), (5) Duparquetioideae LPWG (revised circumscription) and (6) Papilionoideae DC.

Here, we provide a comprehensively updated synthesis of EFNs in Leguminosae, investigating their systematic distribution and the diversity of their locations, morphology and anatomy. We document the occurrence and diversity of EFNs at the generic level, including numerous new generic records of EFN occurrence, and present a comprehensive phylogenetic overview of EFNs across the family, placed within the context of the new subfamily classification and updated generic delimitation based on Legume Phylogeny Working Group (2017).

The term EFN is here used in the broad sense of Elias and Gelband (1976), i.e. including nectaries on floral parts that do not participate in pollination. In a study drawing on all available literature on EFNs, it is important to define the scope of the structure encompassed by the term ‘nectary’. Schmid (1988, p. 187) defined the nectary as ‘a more or less localized, multicellular glandular structure that occurs on vegetative or reproductive organs and that regularly secretes nectar, a sweet solution containing mainly sugars and generally serving as a reward for pollinators or for protectors (e.g., ants) against herbivores, or, in carnivorous plants, as a lure for animal prey’. Mckey (1989) proposed that, for a secretory structure to be considered an EFN, it must meet one or more of the following three criteria: (i) nectar secretion documented, (ii) ant visitation and (iii) homology apparent with nectary glands in related genera. We suggest adding a fourth criterion, as defined by Schmid (1988), namely, that EFNs are localised structures that never extend over the entire leaf or foliar organs (as can be the case for glandular trichomes).

Materials and methods

We compiled a list of legume genera possessing EFNs (Table 1) on the basis of literature reports, herbarium specimens and observations of cultivated and wild plants by the authors or, in some cases, other researchers, during the past 10 years. We have attempted to confirm all published records of EFNs by using also published images, scientific illustrations, and reliably identified and high-quality photographs supplied by colleagues, in addition to herbarium specimens and living plants. Whenever possible, original field observations were documented with colour photographs and verified by presence of a nectar droplet, foraging ants or both. For each genus, we note the location(s) of EFNs in terms of the main plant organ bearing the secretory structure (e.g. stipules, leaves, inflorescences) and provide a description, with further details, on the position and morphology. We do not review reports of secretion of floral nectaries that continue to secrete post-anthesis and, thus, attract ants during fruit development, despite the similar ecological role of such post-floral nectar secretion to that of EFNs. Separately, we list taxa in which EFNs are explicitly reported to be absent, and taxa in which their presence is considered doubtful, where descriptions are inconclusive or reports are contradictory. We compared our total number of EFN-bearing genera with totals listed in previous accounts.

We follow the subfamily classification of Legume Phylogeny Working Group (2017), and lists of accepted genera of Lewis *et al*. (2005) and updates in Lewis *et al*. (2013) and Legume Phylogeny Working Group (2017), which already encompass the revised generic systems of *Vigna* by Delgado-Salinas *et al*. (2011), *Paloue* by Redden *et al*. (2018), and the Caesalpinia group by Gagnon *et al*. (2015, 2016). New genera published after Legume Phylogeny Working Group (2017), such as *Parasenegalia* and *Pseudosenegalia* (Seigler *et al*. 2017) and *Lachesiodendron* (Ribeiro *et al*. 2018), were also included. In several cases, known issues of non-monophyly of genera were taken into account when assessing occurrence of EFNs (e.g. *Prosopis*; see Table 1). For the *Bauhinia* alliance, we discuss the occurrence of EFNs in relation to the forthcoming phylogenetic analysis (C. Sinou and A. Bruneau, unpubl. data). We follow the new tribal classification of Detarioideae (de la Estrella *et al*. 2018), whereas we omitted tribes in Caesalpinioideae because of the limitations and rampant non-monophyly of the current tribes (Legume Phylogeny Working Group 2013), but instead indicated robustly supported clades where necessary (e.g. the mimosoid clade; Legume Phylogeny Working Group 2017). Tribes of Papilionoideae follow Lewis *et al*. (2005).

To assemble an account of the main morphological and anatomical categories of EFNs, 32 species from 18 genera (including new reports) were studied by scanning electron microscopy (SEM) and light microscopy of histological sections. A complete list of the species studied is found in ‘Specimens studied and voucher information’ section in the Supplementary material to this paper. Plant material for SEM and light microscopy analyses was fixed in formaldehyde–acetic acid–70% ethanol (FAA, 5 : 5 : 90), dehydrated and embedded in paraffin (Johansen 1940). Transverse and longitudinal serial sections between 5–7 and 10 μm thick were cut with a rotary microtome (Microm, Walldorf, Germany). Histological sections were stained with two different combinations, namely, safranin–astra blue (Luque *et al*. 1996) or ruthenium red–toluidine blue (Weber and Igersheim 1994). For SEM, samples were prepared following standard procedures of dehydration through a graded acetone series, following critical-point drying using liquid CO_2 and sputter-coating with gold or palladium. Gold-sputtered samples were examined and photographed with a Jeol LV 5800 SEM (20 kV), at the Electron Microscopy Service of the Universidad Nacional del Nordeste (Corrientes, Argentina), and with a Hitachi SU510 SEM (15 kV)

Table 1. List of genera with extrafloral nectaries (EFNs) in the Leguminosae (Fabaceae)

Genera are ordered by subfamilies and tribes or clades, and alphabetically within the latter; except for Caesalpinioideae, where genera of the mimosoid clade are grouped together. Tribes in Caesalpinioideae are after Legume Phylogeny Working Group (2017), in Detarioideae after de la Estrella *et al*. (2018) and in Papilionoideae after Cardoso *et al*. (2012, 2013) and Legume Phylogeny Working Group (2017). Location(s) are ordered following conventional taxonomic descriptions (vegetative parts first). Categories follow the order of the proposed classification. Descriptions synthesise available information on position and morphology, and also include notes by the authors on monophyly or paraphyly, or other relevant issues

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Cercidoideae							
	Bauhinia L. *s.str.*	Stipules, prickles, leaves (?), inflorescences	PA, unknown	Embedded, unknown	Intrastipular secretory structure or as a secretory prickle. In *B. variegata* also observed in the inflorescence, laterally to the bracteoles, but secretory unit unknown (this study). Furthermore, Baker *et al*. (1978, table 1, p. 324) reported EFNs 'on rachis of compound leaf' in *B. pauletia*, but no other detail is provided nor was this report confirmed.	Baker *et al*. (1978); Oliveira and Leitão-Filho (1987); Rezende *et al*. (1994); Oliveira and Pie (1998); da Fonseca Vaz and Tozzi (2003, 2005); Oliveira and Freitas (2004); Machado *et al*. (2008); Melo *et al*. (2010*a*, 2010*b*); Gonzalez and Marazzi (2018); Pereira *et al*. (2018); this study	Fig. 5A–D, 8
Detarioideae							
Afzelieae	*Afzelia* Sm.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; tiny, circular, called 'knotted vein glands' by Hawthorne and Jongkind (2006, p. 837).	Hawthorne and Jongkind (2006); this study (based on image of *A. africana* WH470 by William Hawthorne)	Fig. 9A
Amherstieae	*Anthonotha* P.Beauv.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; tiny, circular, like 'knotted vein glands' (cf. Hawthorne and Jongkind 2006).	This study (based on images of *A. macrophylla* WH200703 *and A vignei* WH5682 by William Hawthorne)	Fig. 9B, C
Amherstieae	*Berlinia* Sol. ex Hook.f.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; tiny, circular, shallow craters, often with a distinct rim; up to 15 per leaflet. However, according to Hawthorne and Jongkind (2006), there are no 'knotted vein glands' in West African species.	MacKinder and Pennington (2011)	
Amherstieae	*Brachystegia* Benth.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; tiny, circular, like 'knotted vein glands' (cf. Hawthorne and Jongkind 2006).	This study (based on images of *B. bussei* EM0136 and *B. leonensis* WH (no number) by William Hawthorne)	Fig. 9D
Amherstieae	*Brownea* Jacq.	Shoot buds, bracts	Unknown	Unknown	Morphology description unavailable, but Büsgen (1903) describes that young shoots develop from buds that secrete conspicous amounts of nectar that are visited by many ants. No structures are documented on leaves.	Büsgen (1903); Mckey (1989); Redden and Herendeen (2006: no EFNs on leaves)	
Amherstieae	*Cynometra* L.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; small disc-shaped, nearby the veins.	A. Radosavljevic and I. Coutinho (unpubl. data, and provided image of *C. ramiflora*)	Fig. 5H, 9F, G
Amherstieae	*Didelotia* Baill.	Leaves	PA	Flat	On the abaxial side of the leaflet lamina; tiny, circular, like 'knotted vein glands' (cf. Hawthorne and Jongkind 2006).	This study (based on image of *D. idae* WH304 by William Hawthorne)	Fig. 9H, I

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Amherstieae	*Gilbertiodendron* J. Léonard (incl. *Pellegriniodendron*)	Leaves	PA	Elevated, flat	Along the margin of the leaflet blade and also apically; elevated, rounded, globose, greenish or reddish when young. Only in *G. diphyllum* (=*Pellegriniodendron diphyllum*) they are in the leaflet lamina; flat, tiny and circular in the middle of a stellate nervation pattern (see also fig. 1, 2 in de la Estrella *et al*. 2012). [Note: the marginal ones have been mentioned also as possible hydathodes, but with no anatomical analysis (e.g. Léonard 1957; Schnell *et al*. 1963).]	Léonard (1957; cited in Mckey 1989); Schnell *et al*. (1963); Koptur (1992a); de la Estrella *et al*. (2012); this study (based on images of *G. preussii* WH137 and *G. splendidum* WH194 by William Hawthorne)	Fig. 9J, K
Amherstieae	*Humboldtia* Vahl	Stipules, leaves, bracts, bracteoles	PA, unknown	Flat, unknown	On the lamina of each of the two pairs of leaflets (in *H. brunonis*); disc-shaped (flat). Also, on stipules and on bracts and bracteoles of inflorescences the flowers of which are still in the bud stage, but no anatomical or morphological description available for EFNs on these locations, meaning that it is not clear whether these are, in structure, similar to or different from the leaf EFNs.	Bower (1887); Mckey (1989); Gaume *et al*. (2005); Shenoy *et al*. (2012); Chanam *et al*. (2014, 2015)	Fig. 5I
Amherstieae	*Hymenostegia* Harms	Leaves	PA	Flat	On the abaxial side of the leaflet lamina, generally found on the leaflet base; tiny, circular, called 'knotted vein glands' by Hawthorne and Jongkind (2006, p. 833).	Hawthorne and Jongkind (2006), this study (based on image of *H. afzelii* WH154 by William Hawthorne)	Fig. 9M
Amherstieae	*Isomacrolobium* Aubrév. & Pellegr.	Leaves	PA	Flat	On the leaflet lamina; tiny, circular, in the middle of a stellate venation pattern.	This study (based on image of *I. elongata* GU1732, GU1945 by William Hawthorne)	Fig. 9N
Amherstieae	*Leonardoxa* Aubrév.	Leaves	PA	Embedded	On abaxial side of leaflet lamina, near the leaf base; disc-shaped, embedded in the leaf mesophyll, with a pore opening to the abaxial surface.	Elias (1980); Mckey (1989)	Fig. 5E, F, 9O, P
Amherstieae	*Loesenera* Harms	Leaves	PA	Flat	On the abaxial side of the leaflet lamina, generally found on the leaflet base; tiny, circular, called 'knotted vein glands' by Hawthorne and Jongkind (2006, p. 837).	Hawthorne and Jongkind (2006)	
Amherstieae	*Paloue* Aubl.	Leaves	PA	Flat	On the leaf lamina base, crater-like glands on the base of the leaf lamina; morphology not further described unknown (fig. 26 in Redden *et al*. 2018).	Redden and Herendeen (2006); Redden *et al*. (2018)	

Amherstieae	*Plagiosiphon* Harms	Leaves	PA	Embedded	Mckey (1989, p. 686) observed ants on small and inconspicuous foliar nectaries, similar in structure and location to those of *Leonardoxa africana.* Morphological and anatomical description unavailable, but inferred by comparison with *L. africana* (this study).	Mckey (1989)	
Detarieae	*Copaifera* L.	Stipules, leaves	PA	Elevated	Along the edges of the stipules and at the base (margin) of the leaflet blade.	Léonard (1957; cited also by Paiva 2009, in his study on *Copaifera langsdorfii*); Schnell *et al*. (1963); Oliveira and Isaias (2010); this study (based on image of *C. salikounda* WHb40 by William Hawthorne)	Fig. 9E
Detarieae	*Daniellia* Benn.	Leaves	PA	Flat	On leaf rachis, in pairs, sunken, between insertion point of all leaflet pairs or only between proximal leaflet pairs. Anatomical description unavailable, bur morphology is suggesting flat type. Often reported to be visited by ants, or ants found even on herbaria specimens.	de la Estrella *et al*. (2010, including fig. 3d, 5e, 6b, 8c, 9e, 10c, 15c, 16d); M. de la Estrella (pers. comm.)	
Detarieae	*Hymenaea* L.	Leaves	PA	Flat	In the leaf lamina (many per leaflet); disc-shaped with embedded tissue and nectar accumulating under cuticula.	Schnell *et al*. (1963); Paiva and Machado (2006); Machado *et al*. (2008); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 9L
Saraceae	*Saraca* L.	Leaves	PA	Unknown	On the leaflet blade margin. Illustrated in fig. 8-1 (Moog 2009, p. 219), but structure of EFNs unavailable, possibly elevated by comparison with *Copaifera* and *Gilbertiodendron* (this study).	Fiala and Linsenmair (1995); Moog (2009)	
Caesalpinioideae							
Caesalpinieae	*Batesia* Spruce ex Benth.	Leaves	PA	Elevated	On rachis on adaxial surface between leaflets (first pair of leaflets may fall but not the respective EFNs); sessile, rounded, and convex shape similar to elevated EFNs in some *Senna* (this study). [Note: Lersten and Curtis (1996, p. 29) cited 'small clavate to weakly capitate trichomes on both surfaces' of leaflets, but most likely not nectariferous.]	Herendeen *et al*. (2003); Rodrigues *et al*. (2012); this study (based on images of voucher specimen M. M. T. Cotta 1145)	Fig. 10A
Caesalpinieae	*Biancaea* Todd	Leaves	Unknown	Unknown	On rachis, but no description of morphology available in Pemberton (1990).	Pemberton (1990, as *Caesalpinia japonica*)	
Caesalpinieae	*Caesalpinia* L. (s.str.)	Stipules, leaves, bracts, pedicels	AZ	Non-differentiated	Nectar accumulates at the base of pedicel (at the bud stage and in open flowers), corresponding to the insertion area of (caducous) bracts and their abscission scar, and near stipules. No external structure visible.	Gagnon *et al*. (2016, fig. 11); this study	Fig. 10B, C

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Caesalpinieae	*Erythrophleum* Afzel. ex R.Br.	Leaves	PA	Elevated	On leaf rachis between leaflets, rather cryptic, with a small domed structure with a central pore, the rest of the structure is embedded within the rachis.	Pascal *et al*. (2000)	
Caesalpinieae	*Gelrebia* E.Gagnon & G. P.Lewis	Pedicels	AZ	Non-differentiated	Nectar accumulates at the base of pedicel (at least at the bud stage, based on fig. 11J in Gagnon *et al*. 2016); perhaps in other locations too. No external structure visible, though anatomy unknown.	Gagnon *et al*. (2016, fig. 11)	
Caesalpinieae	*Libidibia* (DC.) Schltdl. (incl. *Stahlia* Bello)	Pedicels	AZ	Non-differentiated	Modified floral pedicels with an elaborate group of cells (fig. 3A, B in Melo *et al*. 2010*b*).	Melo *et al*. (2010*a*, 2010*b*)	
Cassia clade	*Chamaecrista* Moench	Leaves	PA	Elevated	On the petiole and along the rachis between leaflets; stalked or sessile.	Irwin and Barneby (1982); de Souza Conceição *et al*. (2009); Melo *et al*. (2010*a*, 2010*b*); Coutinho *et al*. (2012); Coutinho and Meira (2015); Silva *et al*. (2017); Gonzalez and Marazzi (2018); this study	Fig. 6E, 10D, E
Cassia clade	*Senna* Miller	Stipules, leaves, inflorescences, bracts, sepals	PA, AZ, FO	Elevated, flat, non-differentiated, formless	Elevated EFNs have a convex shape, are raised (stalked or sessile) on the petiole only or also along the rachis between leaflets, as modified mucro (only in *S. scabriuscula*); sometimes also at the base of pedicels, subtended by reduced bracts. Flat EFNs are in form of modified stipule lobes, with the secretory lobe of a different colour. Non-structural EFNs occur at the abscission zone of bracts; formless EFNs occur on the dorsal side of bracts and sepals. [Note: elevated EFNs occur exclusively in the EFN clade and the other kinds occur in species of Clade II, whereas EFNs are apparently absent from the remaining Clades I and III (Marazzi *et al*. 2013*b*); Marazzi *et al*. (2013*b*) did not formally separate formless from non-structural EFNs.]	Irwin and Barneby (1982); Marazzi *et al*. (2006), Marazzi and Sanderson (2010); Marazzi *et al*. (2013*b*); Gonzalez and Marazzi (2018); this study	Fig. 4A–C, 5J–O, 6B, G–J, L–O, 10F–N
Cassia clade	*Vouacapoua* Aubl.	Leaves	PA	Elevated	On petiole and also on the rachis between first pair of leaflets; sessile, rounded, apparently convex in shape.	Herendeen *et al*. (2003); this study (based on image of voucher specimen DC3450)	Fig. 10O, P

Mimosoid clade	*Abarema* Pittier	Leaves	PA	Elevated	One, on petiole, almost always between or close below proximal pair of pinna-pulvinules, often one smaller one between further pairs and nearly always between the last pairs of leaflets. Campanulate to cupular, patelliform or verruciform, only rarely stipitate, sometimes immersed. In two species, the nectaries are highly modified: either into a conspicuous coloured funnel-shaped nectary, up to 12 mm long and yellowish on fresh material, in *A. adenophora*, or a campanulate nectary becoming subligneous, up to 11 mm, in *A. macradenia*. [Note: *Abarema* is not monophyletic according to Iganci *et al*. (2016).]	Barneby and Grimes (1996); this study	Fig. 11A
Mimosoid clade	*Acacia* Mill. (*s.str.*)	Leaves	PA	Elevated, flat	Gland-like, on the petiole, rachis between leaflets or pinnae; apparently cryptic on phyllode margin. According to Boughton (1981, 1985), EFNs of phyllodineous and bipinnate acacias are of three types: porate, non-porate and flat. [Note: apparently almost universal across the genus (see Maslin *et al*. 2001, for details).]	Zimmermann (1932, p. 176); Boughton (1981, 1985); Maslin *et al.* (2001); this study	Fig. 11B
Mimosoid clade	*Adenopodia* (=*Pseudoentada*) C. Presl.	Leaves	PA	Elevated	Near the base of the petiole and often between pinnae pairs and leaflet pairs as well, sessile or raised, tack-shaped or bathtub-shaped, crateriform. Reduced leaves (reduced bracts) at the base of the inflorescence spikes usually bear enlarged nectaries as well.	Lewis and Elias (1981, as *Pseudoentada*); this study	
Mimosoid clade	*Alantsilodendron* Villiers	Leaves	PA	Elevated	On petiole, most often inserted between the lower pair of pinnae, sometimes between more distal pinnae as well; sessile, orbicular, cupulate, crateriform or cylindrical.	Villiers (2002*b*); this study	
Mimosoid clade	*Albizia* Durazz.	Leaves	PA	Elevated	Near, below or well below mid-petiole, sometimes adjacent to leaf pulvinus, sessile, round or vertically elongate, shallow cupular, shallowly patelliform, or almost plane, sometimes immersed in petiolar groove and reduced to a minute pore, or almost obsolete, sometimes smaller nectaries at insertion of 1–4 furthest pairs of pinnae, a much smaller nectary at tip of most pinnae, or between 1 and 2 furthest pairs of leaflets. [Note: *Albizia* is not monophyletic and will be split up in the near future, E. J. Koenen, unpubl. data.]	Barneby and Grimes (1996); Pemberton (1990); Koptur (1992*a*); this study	Fig. 11C

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Anadenanthera* Speg.	Leaves	PA	Elevated	On petiole and rachis, round or oval, subsessile and with a smooth surface, pinkish in young stages.	Lewis and Elias (1981); Machado *et al*. (2008); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 11D
Mimosoid clade	*Archidendron* F.Muell.	Stem or shoot, leaves, bracts	PA	Elevated	Rich diversity (illustrated in Nielsen *et al*. 1984). On petiole, in the form of modified stipules, and (in series *Stipulatae*) on the floral bracts. Petiole glands sessile or stipitate, raised, circular or linear-oblong and concave, flat or urceolate. Occasionally nest-shaped with the upper part of the gland bent over the cavity as a lid, or narrow slit-like and not raised. Nectaries on stipules also occur in the genus where the stipules are replaced by glands that are in shape and form similar to those on the petiole, sometimes with a downward pointing acumen (fig. 16 in Nielsen 1992). Floral bracts in series *Stipulatae* with ring-shaped nectaries near the base (Nielsen *et al*. 1984; fig. 17 in Nielsen 1992), the nectary well developed, whereas the bract is reduced.	Nielsen *et al*. (1984); Nielsen (1992, including illustrations); Fiala and Linsenmair (1995); So (2004)	
Mimosoid clade	*Archidendropsis* I.C. Nielsen	Leaves	PA	Elevated	On rachises and pinnae, at or slightly below insertion of pinnae, elliptic, circular or triangular, sessile with raised margins.	Nielsen (1992)	
Mimosoid clade	*Balizia* Barneby & J.W. Grimes	Leaves	PA	Elevated	Sessile or shortly stipitate, the first situated either near mid-petiole or between first pinna-pair, others between each pair of pinnae, and yet smaller ones between terminal leaflets. Variable in number, position and form.	Barneby and Grimes (1996); Blüthgen *et al*. (2000)	Fig. 11E
Mimosoid clade	*Blanchetiodendron* Barneby & J.W. Grimes	Leaves	PA	Elevated	Near or above mid-petiole, sessile, cupular or shallow-cupular, minute nectaries at tip of some pinna-rachises, none between pinna-pairs.	Barneby and Grimes (1996)	
Mimosoid clade	*Calliandropsis* H. Hernández & Guinet	Leaves	PA	Elevated	On rachis at the point of insertion of the pinnae, cup-shaped, slightly elevated.	Hernández and Guinet (1990)	
Mimosoid clade	*Calpocalyx* Harms	Leaves, bracts	PA	Elevated	On the petiole and rachis, borne between pinnae pairs on the rachis and between pairs of leaflets as well in some species; not crateriform, usually sunken into the petiole and canaliculate, sometimes a raised pad. EFNs also on bracts (that fall early).	This study (based on Jstor Plants. *Calpocalyx ngounyensis* (P), Le Testu G. M.P.C., #5513, at https://plants.jstor.org/stable/10.5555/al.ap.specimen.p00540576?searchUri=si%3D51%26filter%3Dname%26so%3Dps_group_by_genus_species%2Basc%26Query%3DCalpocalyx%2B, accessed 12 August 2019)	

Mimosoid clade	*Cathormion* Hassk.	Leaves	PA	Elevated	On rachises and pinnae at insertions between pinnae, elliptic to circular, margins raised, slightly concave. [Note: *Cathormion* is non-monophyletic, but both African and Asian elements possess EFNs (Hawthorne and Jongkind 2006, illustrate the EFNs of *C. rhombifolium* and *C. altissimum* from Africa).]	Nielsen (1992)	
Mimosoid clade	*Cedrelinga* Ducke	Leaves	PA	Elevated	At or close below insertion of each pinna-pair, low-convex and wrinkled or sunk into epidermis and amorphous, similar but smaller nectaries between furthest 1 or 2 pairs of leaflets.	Barneby and Grimes (1996); Hawthorne and Jongkind (2006); Muehleisen *et al*. (2016)	
Mimosoid clade	*Chloroleucon* (Benth.) Britton & Rose	Leaves	PA	Elevated	Concave, sessile or almost so, usually near or below mid-petiole, rarely between first (or only) pair of pinnae, smaller nectaries at tip of leaf stalk and pinnae rachises.	Barneby and Grimes (1996); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 11F
Mimosoid clade	*Cojoba* Britton & Rose	Leaves	PA	Elevated	Petiole and at or close below pinna-pairs, exceptionally 1 or 2 on petiole proper, and in some species smaller nectaries on some distal interfoliar segments of pinna-rachises or between some or all leaflet pairs; sessile, cupular, thick-rimmed.	Barneby and Grimes (1997)	
Mimosoid clade	*Cylicodiscus* Harms	Leaves	PA	Elevated	On rachis between the first pair of pinnae; round and sunken.	Lewis and Elias (1981); this study	
Mimosoid clade	*Desmanthus* Willd.	Leaves	PA	Elevated	On petiole and rachis between pinnae or just below; three types (Luckow 1993; nectary morphology may vary within a species): sessile-crateriform (the most common), sessile-flattened (in a few herbaceous species), and stipitate (in a few woody species).	Luckow (1993; with illustrations of the three types of nectary); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 6D, K, 11G–I
Mimosoid clade	*Dichrostachys* (DC.) Wight & Arn.	Leaves	PA	Elevated	At end of rachis between proximal pairs of pinnae, on petiole, sometimes between all pinnae pairs; long and stipitate.	Schnell *et al*. (1963); this study	Fig. 11J
Mimosoid clade	*Ebenopsis* Britton & Rose	Leaves	PA	Elevated	Interpinnal usually at insertion of each pinna-pair, rounded, cupular, thick-rimmed, peg-shaped sessile or short and stoutly stipitate.	Barneby and Grimes (1996); this study	Fig. 11K

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Entada* Adans.	Stem or shoot, bracts	PA	Pit, flat	Generally thought to be absent in *Entada* (and the nested *Elephantorrhiza*), but recorded on stems and floral bracts of *E. phaseoloides* in Australian rainforest as flat or pit (with a large central cavity deeply embedded in twig with a long orifice) nectaries on stem adjacent to junctions of twigs and petioles and floral bracts and producing nectar even on mature twigs. According to Blüthgen and Reifenrath (2003, p. 521), EFN 'on stem adjacent to junctions of twigs or petioles. Nectar is secreted near the top of an elongate elevation. The following two different types of EFN co-occur in the same twig junctions: (1) pit EFN whose large central cavity is deeply embedded into the twig, with a long orifice (300 µm long × 10 µm wide), the orifice opening funnel shaped and depressed into the surrounding epidermis; (2) flattened EFN with irregular palisade parenchyma, collapsed tissue and ruptured cuticle. Additional flattened EFNs occur on a distinct bract on each inflorescence stalk basal to the flowers.' [Note: Blüthgen *et al*. (2004) studied nectar composition in this species.]	Blüthgen and Reifenrath (2003)	Fig. 5G
Mimosoid clade	*Enterolobium* Mart.	Leaves	PA	Elevated	On petiole (adjacent to pulvinus, at mid-petiole, or close to first pinna-pair, below pinnae or between first pair of pinnae), sometimes also between ultimate 3–5 pinna-pairs; cupular, patelliform or mounded, or sunk in petiolar groove, rounded, sessile or slightly elevated.	Croat (1978); Oliveira and Leitão-Filho (1987); Oliveira and Oliveira-Filho (1991); Barneby and Grimes (1996); Machado *et al*. (2008); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 6C, 11L–N
Mimosoid clade	*Faidherbia* A.Chev.	Leaves	PA	Elevated	One or sometimes two, on petiole (adjacent to pulvinus, at mid-petiole, or close to first pinna-pair, below pinnae or between first pair of pinnae), sometimes also between last pinna-pairs; patelliform or mounded.	Illustrated in Lewis *et al*. (2005); this study	

Mimosoid clade	*Falcataria* (I.C.Nielsen) Barneby & J.W. Grimes	Leaves	PA	Elevated	Near mid-petiole or close below first pinna-pair, sessile, oblong to ellipsoid, convex but dimpled, small round button-like nectaries at insertion of furthest 2–4(–5) pinna-pairs, and yet smaller cupular ones on 1–3 furthest segments of pinna-rachises.	Barneby and Grimes (1996); this study (based on leaf image of *F. moluccana* (=*Paraserianthes falcataria*) by Idris Abdul Haris, specimen by Mary C. Merello 3373, available on Tropicos.org. Missouri Botanical Garden, see http://www.tropicos.org/Name/40037248)	
Mimosoid clade	*Gagnebina* Neck. ex DC.	Leaves	PA	Elevated	On petiole, most often inserted between the lower pair of pinnae but sometimes midway on the petiole and sometimes between additional pinnae as well; sessile and cupulate or cylindrical or sometimes urceolate.	Lewis and Guinet (1986); this study	
Mimosoid clade	*Havardia* Small	Leaves	PA	Elevated	Variably placed on petiole half-way between insertion of leaf and 1st pair of pinnae, sometimes below mid-petiole and occasionally at very base or between one or more pairs of pinnae; sessile, crateriform, thick-rimmed, round to oval, sometimes a similar gland at tip of leaf stalk, or between 1–3 furthest pinnae pairs and a minute one at tip of some pinna-rachises.	Barneby and Grimes (1996); this study	Fig. 11O, P
Mimosoid clade	*Hesperalbizia* Barneby & J.W.Grimes	Leaves	PA	Elevated	Below mid-petiole, sometimes close to the leaf pulvinus, sessile, round or elliptic, shallowly concave and commonly a smaller one near tip of petiole and a yet smaller one near tips of pinna rachises.	Barneby and Grimes (1996)	
Mimosoid clade	*Hydrochorea* Barneby & J.W.Grimes	Leaves	PA	Elevated	Petiole, between or close below insertion of first or only pinna pair; either sessile or stipitate (rarely suppressed), the head variably plane, convex or shallow-cupular.	Barneby and Grimes (1996); this study (based on online digital image of the herbarium specimen of *H. corymbosa* by F. W. R. Hostmann 262, available at Tropicos.org. Missouri Botanical Garden, at http://www.tropicos.org/Image/25083)	
Mimosoid clade	*Indopiptadenia* Brenan	Leaves	PA	Elevated	On rachis inserted between the first pair of pinnae, sometimes present at the apex of the petiole, additional nectaries often between the leaflets; plane, oval, pad-like, undifferentiated.	Lewis and Elias (1981); illustrated with photos in Bajpai *et al*. (2014); this study	
Mimosoid clade	*Inga* Mill. (incl. *Affonsea*)	Leaves	PA	Elevated	Almost universal in the genus with normally a single gland between each pair of leaflets, but sometimes 2 or 3 at each point of insertion of the leaflet pairs. Variable in form from pulvinate with a small aperture to flat, patelliform with a broad nectar-secreting surface to cyathiform or funnel-shaped, usually circular. In most extreme development it becomes a long slender stalked structure up to 6 mm long with an unexpanded or minutely cup-shaped head (fig. 155 in Pennington 1997). Stalked form with clavate head only in *I. allenii* (fig. 77 in Pennington 1997).	Schnell *et al*. (1963); Baker *et al*. (1978); Koptur (1984, 1985, 1994); Mckey (1989); Morellato and Oliveira (1991); Pennington (1997) [with illustrations]; Melo *et al*. (2010*a*, 2010*b*); Brenes-Arguedas *et al*. (2008); Bixenmann *et al*. (2011, 2013); this study	Fig. 12A, B

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Kanaloa* Lorence & K.R. Wood	Leaves	PA	Elevated	On rachis, between pinnae pairs; Sessile, cupulate, orbicular or elliptical, the margin hirtellous, the concavity glabrous.	Lorence and Wood (1994); this study	
Mimosoid clade	*Lachesiodendron* P.G. Ribeiro & L.P.Queiroz & Luckow	Leaves	PA	Elevated	On mid-petiole, sessile, discoid; additional smaller one between distal pinnae pair and on the pinna rachis between the proximal and distal pair of leaflets.	Ribeiro *et al.* (2018)	
Mimosoid clade	*Lemurodendron* Villiers & Guinet	Leaves	PA	Elevated	On the rachis between the pinnae pairs; simple mounded.	Villiers and Guinet (1989, illustrated)	
Mimosoid clade	*Leucaena* Benth.	Leaves, bracts	PA	Elevated	On petiole below insertion of first pair of pinnae or on rachis between pinnae pairs, occasionally infrapinnal as well; sessile and mound-shaped or cylindrical, stipitate and peg-shaped. On leaf petioles on partially developed leaves that subtend inflorescences and which apparently terminate development (observed in one species; O. Dorado and K. López, unpubl. data).	Mckey (1989); Hughes (1998); this study	Fig. 6F, 12C–G
Mimosoid clade	*Leucochloron* Barneby & J.W.Grimes	Leaves	PA	Elevated	On rachis, between or close below proximal pinna-pair, but sometimes below mid-petiole; sessile, cupular or almost plane.	Barneby and Grimes (1996)	
Mimosoid clade	*Lysiloma* Benth.	Leaves	PA	Elevated	Near or well above mid-petiole, sessile, either obesely cupular or mounded small-pored, and smaller ones often between some distal pinna-pairs and towards tip of pinna-rachises.	Zimmermann (1932); Barneby and Grimes (1996); Moya-Raygoza and Larsen (2001); Gale and Pennington (2004); this study	Fig. 6A, 12H
Mimosoid clade	*Macrosamanea* Britton & Killip	Leaves, bracts	PA	Elevated	On petiole sessile, scuteliform or patelliform or shallowly cupular, the first situated either next to leaf pulvinus or between first pinna pair, similar nectaries often between further pinna pairs and near tip of pinna rachises. Also, on some or all floral bracts of the capitulum in most species and this unique within neotropical Ingeae, but also seen in some Asiatic species of *Archidendron.*	Barneby and Grimes (1996); this study	Fig. 12I, J
Mimosoid clade	*Mariosousa* Seigler & Ebinger	Leaves	PA	Elevated	On petiole just below or between pairs of pinnae; crateriform, rounded.	This study	Fig. 12K
Mimosoid clade	*Microlobius* (=*Goldmania*) C.Presl	Leaves	PA	Elevated	On rachis between pinnae pairs and between the leaflets; sessile, cup-shaped, crateriform.	This study (based on herbarium specimen Di Giacomo 524 [CTES] of *Microlobius foetidus* subsp. *paraguensis*, fig. X).	Fig. 12L

Mimosoid clade	*Mimosa* L.	Leaves	PA	Elevated	Usually on the petiole below the insertion of the first pair of pinnae, but between the proximal pair of pinnae in some species; sessile and cupular or cylindrical with a very small opening. [Note: only a small minority of species (~15 spp.) have EFNs and that these are confined to the monophyletic section *Mimadenia*, which is sister to the rest of the genus, i.e. presence of an EFN within *Mimosa* is plesiomorphic, as shown by Simon *et al*. (2011). Most of species are eglandular or have a nectary that is reduced to a minute obsolete spicule, although Gonzalez and Marazzi (2018) have found small, normally developed nectaries in *M. bifurca* of section *Batocaulon*.]	Hall (1762); Zimmermann (1932); Schnell *et al*. (1963); Barneby (1991); Morellato and Oliveira (1991); Pascal *et al*. (2000); Simon *et al*. (2011); Gonzalez and Marazzi (2018); this study	Fig. 13A
Mimosoid clade	*Mimozyganthus* Burkart	Leaves	PA	Elevated	On rachis between pinnae, sessile, discoid, gland-like.	Elias (1983); this study	
Mimosoid clade	*Neptunia* Lour.	Leaves	PA	Elevated	Present or absent, between proximal pair of pinnae most often, sometimes between distal pairs as well; crateriform or cup-shaped, flattened in some species, sessile, not sunken.	Zimmermann (1932); Melo *et al*. (2010*a*, 2010*b*); this study	
Mimosoid clade	*Newtonia* Baill.	Leaves	PA	Elevated	Between the proximal pair of pinnae and usually between all pairs, also present between leaflets in some species, sessile or stipitate, crateriform, cylindrical, mound-shaped or barrel-shaped in one species.	Lewis and Elias (1981); this study	
Mimosoid clade	*Painteria* Britton & Rose	Leaves	PA	Elevated	Below proximal pinna-pair at tip of petiole, none on pinna-rachises, round, dimpled, shortly stout-stipitate (drum-shaped) or subsessile.	Barneby and Grimes (1996); this study	Fig. 13B
Mimosoid clade	*Parapiptadenia* Brenan	Leaves	PA	Elevated	On petiole, half way between first pair of pinnae and base of petiole, near the base of the petiole, or between the proximal pair of pinnae, also between upper pinnae on some; sessile or stipitate and tack-shaped, crateriform or rounded, or sunken and crateriform to vagiform, may be very elongated.	Lewis and Elias (1981); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 13C
Mimosoid clade	*Pararchidendron* I. C. Nielsen	Leaves	PA	Elevated	At or below mid-petiole below pinnae, also between upper pinnae, sessile, circular, flat to concave.	Nielsen *et al*. (1983); Nielsen (1992); this study (based on the New South Wales Flora online for *P. pruinosum* at http://plantnet.rbgsyd.nsw.gov.au/cgi-bin/NSWfl.pl?page=nswflandlvl=spandname=Pararchidendron~pruinosum)	

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Parasenegalia* Seigler & Ebinger	Leaves	PA	Elevated	On petiole, or between first pair of pinnae or also between terminal pair of pinnae; sessile, crateriform, round to oval.	Seigler *et al.* (2017)	
Mimosoid clade	*Paraserianthes* I.C. Nielsen	Leaves	PA	Elevated	Mid-petiole, circular to elliptic, ususally raised, convex or concave, smaller glands at insertions of distal pinna-pairs.	Nielsen (1992); Nielsen *et al.* (1983); Barneby and Grimes (1996)	
Mimosoid clade	*Parkia* R.Br.	Leaves	PA	Elevated	On petiole below pinnae, between pinnae on primary rachis, sometimes on secondary rachis between leaflets; sessile, round, heart-shaped (double), or elliptical.	Schnell *et al.* (1963); Fiala and Linsenmair (1995); this study	
Mimosoid clade	*Pentaclethra* Benth.	Stem or shoot	PA	Elevated	On the node: in young shoots clearly laterally to the stipule base that runs down the shoot axis, whereas the leafy lamina falls off during development; elliptic, cup-shaped (convex). In older shoots, laterally to the scar of the fallen stipule. No EFNs on leaf petiole or rachis (absence confirmed in *P. macroloba*, this study, and in *P. macrophylla*, Hawthorne and Jongkind 2006).	Baker *et al.* (1978); Hartshorn (1983); Janzen and Carroll (1983); Bennett and Breed (1985); Mckey (1989); this study	Fig. 13D, E
Mimosoid clade	*Piptadenia* Benth. (excl. *Goldmania*)	Leaves	PA	Elevated	On petiole below pinnae, between proximal pair of pinnae or both, and often between distal pairs as well, sometimes between leaflets, sometimes scattered on rachis between pinnae; highly variable in form as well, sessile or raised, volcaniform, crateriform, club-shaped, flattened.	Lewis and Elias (1981); Melo *et al.* (2010*a*, 2010*b*); this study	
Mimosoid clade	*Piptadeniastrum* Brenan	Leaves	PA	Elevated	On the petiole; crateriform. *Piptadeniastrum africanum* sometimes (but not always) has a crateriform gland on the petiole (Hawthorne and Jongkind (2006; EFN illustrated on p. 859). The reports of absence (Lewis and Elias 1981, cited in Mckey 1989) presumably derive from the fact that this species only has EFNs sometimes.	Hawthorne and Jongkind (2006; EFN illustrated on p. 859)	
Mimosoid clade	*Piptadeniopsis* Burkart	Leaves	PA	Elevated	On leaf rachis between first and last pairs of pinnae, and others between leaflets at apex of pinnular rachis; sessile, circular.	Burkart (1944)	

Mimosoid clade	*Pithecellobium* Mart.	Leaves	PA	Elevated	Between each pinna-pair and also (except *P. histrix*) at tip of all pinna-rachises, and sometimes between leaflet pairs; cupular, thick-rimmed, either sessile or shortly and stoutly stipitate (drum-shaped or turbinate). Very large cupular nectary in *P. macradenium* (up to 7.4 mm in diameter; Elias 1972).	Böhmker (1917, as *Pithecolobium saman*); Zimmermann (1932, as *Pithecolobium* Benth); Baker *et al.* (1978, as *Pithecolobium*); Barneby and Grimes (1997); Elias (1972); Fiala and Linsenmair (1995); Melo *et al*. (2010*a*, 2010*b*); this study	
Mimosoid clade	*Pityrocarpa* (Benth.) Britton & Rose	Leaves	PA	Elevated	Near base of petiole, also on pinnae between 1–3 terminal pairs of leaflets on some, occasionally between uppermost pinnae pairs as well, and often between terminal pairs of leaflets; rounded or crateriform.	Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 13F
Mimosoid clade	*Plathymenia* Benth.	Stem or shoot, stipules, leaves	PA	Elevated	On rachis between leaflet pairs; also occurring on the stem (shoot) where stipules should be (L. Borges, unpubl. data). In some plants, occasionally with an inconspicuous lump on the petiole, these actually cited on stems by Machado *et al*. (2008, their Table 1, but with no other details).	Lewis and Elias (1981); Warwick and Lewis (2003); Machado *et al*. (2008); L. Borges (unpubl. data)	
Mimosoid clade	*Prosopidastrum* Burkart	Stipules(?), leaves	PA, unknown	Elevated, unknown	Elevated EFNs between pinnae; sessile or stipitate, orbicular, cup-shaped or with a small pore. Stipule bases are described as 'glandular' in some species by Palacios and Hoc (2005), but no anatomical description available.	Lewis and Elias (1981); Palacios and Hoc (2005); this study (based on online image of Isotype of *Prosopidastrum dehiscens*, herbarium specimen Palmer, E., #241, at herbarium (K), at https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000503058?searchUri=filter%3Dname%26so%3Dps_group_by_genus_species%2Basc%26Query%3DProsopidastrum)	
Mimosoid clade	*Prosopis* L.	Leaves	PA	Elevated	On rachis between proximal pair of pinnae, sometimes between distal ones as well; orbicular, cup-shaped. [Note: *Prosopis* is non-monophyletic and *Prosopis africana* does not belong with the rest of *Prosopis*, but both genera have EFNs. *Prosopis africana* will need to be segregated as a new genus and has EFNs at insertion of pinnae and also often between leaflet pairs (illustrated in Brenan 1959, fig. 10, p. 35).]	Pemberton (1988); Melo *et al*. (2010*a*, 2010*b*); this study	Fig. 13G–I
Mimosoid clade	*Pseudopiptadenia* Rauschert (=*Monoschisma*)	Leaves	PA	Elevated	Between proximal pair of pinnae or below on the petiole, often between distal pinnae and even between leaflets; sunken, stalked or sessile, crateriform or flattened.	Elias (1983); this study	Fig. 13J

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Pseudoprosopis Harms*	Stem or shoot	AZ	Non-differentiated	On the stipular scars (in some species; Villiers 1989) or the twigs near the base of the stipules (in *P. sericeus*; Hawthorne and Jongkind 2006); described as 'with dark ribs and more or less flattened sides' (in *P. sericeus;* Hawthorne and Jongkind 2006, illustrated on p. 861), but no other anatomical details available.	Villiers (1989); Hawthorne and Jongkind (2006)	
Mimosoid clade	*Pseudosamanea* Harms	Leaves	PA	Elevated	On the petiole, at or a little above or below mid-petiole; sessile, elliptic or almost round, shallowly concave, thin-margined. Sometimes a second smaller nectary near it and another at or close to leaf stalk distal end, yet smaller ones on 2 or 3 furthest segments of pinna-rachis.	Barneby and Grimes (1996)	
Mimosoid clade	*Pseudosenegalia* Seigler & Ebinger	Leaves	PA	Elevated	On rachis between first pair of pinnae; sessile, crateriform, round to oval.	Seigler *et al.* (2017)	
Mimosoid clade	*Pujunba* Britton & Rose	Leaves	PA	Elevated	On petiole or on rachis as well, between pairs of pinnae and between each pair of leaflets; sessile, immersed, shallowly cupular or crateriform with thickened rim, suborbicular.	Barneby and Grimes (1996)	
Mimosoid clade	*Samanea* (Benth.) Merr.	Leaves	PA	Elevated	Close below first, furthest, and often all pinna-pairs, sessile, shallowly cupular, thick-rimmed, round or bluntly triangular. Similar but smaller nectaries on pinna-rachises close below each leaflet pair. [Note: *Samanea* is not monophyletic, but neotropical and Old World elements possess EFNs (Hawthorne and Jongkind 2006).]	Schnell *et al.* (1963); Barneby and Grimes (1996); Hawthorne and Jongkind (2006)	
Mimosoid clade	*Sanjappa* E.R.Souza & M.V.Krishnaraj	Leaves	PA	Elevated	At the end of the petiole, circular, slightly raised (described and illustrated in de Souza *et al.* 2016).	de Souza *et al.* (2016)	
Mimosoid clade	*Schleinitzia* Warb. ex L.I. Nevling & C.J. Niezgoda	Leaves	PA	Elevated	On petiole half-way between insertion of leaf and proximal pair of pinnae or between first pair of pinnae only, or between all pairs of pinnae; sessile, crateriform, round to oval.	Nevling and Niezgoda (1978, illustrates EFNs); this study	
Mimosoid clade	*Senegalia* Raf.	Leaves	PA	Elevated	On petiole, half-way between insertion of leaf and first pair of pinnae or between one or more pairs of pinnae; sessile, crateriform, round to oval.	Melo *et al.* (2010*a*, 2010*b*); this study	Fig. 13K
Mimosoid clade	*Serianthes* Benth.	Leaves	PA	Elevated	On petiole, on lower portion or mid-petiole; raised, cushion-shaped or concave. Also, smaller ones at point of insertion of each pinna-pair and 1–5 distal pairs of leaflets; sessile, crateriform, round to oval.	Zimmermann (1932); Nielsen *et al.* (1983); Nielsen (1992)	

Mimosoid clade	*Sphinga* Barneby & J.W. Grimes	Leaves	PA	Elevated	Below or near mid-petiole; sessile, shallowly cupular or patelliform and thick-rimmed, round or elliptic. None between pinnae, but sometimes a small one on furthest segment of pinna-rachises.	Barneby and Grimes (1996)	
Mimosoid clade	*Stryphnodendron* Mart.	Leaves	PA	Elevated	On petiole, usually half-way to and sometimes near the proximal pair of pinnae, additional ones often distally on the rachis and pinna, usually not between the pinnae or leaflets, but on the rachis or pinna and inserted between contiguous pairs; verrucate or planar, rarely crateriform.	Machado *et al.* (2008); this study	Fig. 13L–N
Mimosoid clade	*Thailentadopsis* Kosterm.	Leaves	PA	Elevated	Between pinna-pairs, and also smaller similar nectaries on pinna-rachises between leaflet pairs; substipitate or stipitate, round, urceolate, or long-stalked and trumpet-shaped.	Nielsen (1981, 1985, there under *Pithecellobium*)	
Mimosoid clade	*Vachellia* Wight & Arn.	Leaves	PA	Elevated	On petiole and on rachis between pinnae leaflets.	Baker *et al.* (1978, as *Acacia farnesiana*); Pascal *et al.* (2000, as *Acacia sphaerocephala*); Gadd *et al.* (2001, as *Acacia drepanolobium*); this study (*V. stricta*)	Fig. 13O
Mimosoid clade	*Viguieranthus* Villiers	Leaves	PA	Elevated	One between the single pair of pinnae, sessile or very short stipitate (cylindrical), round, narrowly cupular.	Illustrated in Lewis *et al.* (2005); Villiers (2002*a*)	
Mimosoid clade	*Wallaceodendron* Koord.	Leaves	PA	Elevated	On rachis, between pinnae and leaflets, elliptic or round, raised and convex.	Nielsen (1992); This study (based on photograph by David Stang available on Tropicos.org. by the Missouri Botanical Garden, see http://www.tropicos.org/Image/100122410)	
Mimosoid clade	*Xerocladia* Harv.	Leaves	PA	Elevated	Between the proximal pinnae; sessile, cupulate.	Lewis and Elias (1981); Melo *et al.* (2010*a*, 2010*b*); this study	
Mimosoid clade	*Xylia* Benth.	Leaves	PA	Elevated	On rachis, between the pinnae, usually also between distal pairs of leaflets, and sometimes between all pairs of leaflets; round, mound-shaped.	Brenan (1959, illustrated on p. 34); this study	
Mimosoid clade	*Zapoteca* H.M.Hern.	Leaves	PA	Elevated	Between first pair of pinnae and less frequently also between distal pairs of leaflets, cup-shaped or cylindrical. [Note: present only in 3 of the ~20 species, with the phylogeny of Ferm (2019) implying a single evolutionary loss of EFNs within the genus. See main text.]	Hernández (1989)	

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Mimosoid clade	*Zygia* P.Browne (incl. *Marmaroxylon*)	Stem or shoot, leaves	PA	Elevated	On petiole and on rachis between each pair of pinnae, on pluripinnate leaves at or close below first and often further pinna-pulvini, and sometimes smaller ones between further leaflet pairs, all sessile, shallowly cupular, plane or low-convex. According to Blüthgen and Reifenrath (2003) on both stem and rachis, describing them as 'very large and conspicuous, elevated, cup-shaped (1–2 mm in diameter) [...] strongly vascularised, the vessels leading into a brightly coloured, multi-layered, small-celled tissue including the epidermis (Fig. 3B). This tissue is conspicuously dark brown in its central area of secretion.' [Note: Lewis *et al*. (2005) listed genus *Marmaroxylon* Killip, which is here treated as a synonym of *Zygia* following Barneby and Grimes (1997).]	Barneby and Grimes (1997); Blüthgen and Reifenrath (2003; as *Archidendron ramiflorum*=*Zygia ramiflora*); Muehleisen *et al*. (2016); this study	Fig. 13P
Papilionoideae							
Angylocalyceae	*Alexa* Moq.	leaves, bracts	PA	Flat(?)	Leaves bear tiny round EFNs and bracts subtending flowers are covered in up to 20 tiny nectaries, illustrated on p. 9, letter H (*A. canaracunensis*; Lewis and Owen 1989) that resemble flat EFNs of *Castanospermum.*	Lewis and Owen (1989)	
Angylocalyceae	*Castanospermum* A. Cunn. ex Hook.	Stem or shoot, leaves	PA	Flat	Scattered over the stem, rachis and leaflets, illustrated and described by Blüthgen and Reifenrath (2003) as 'visible as elongate elevations stretching along the axis (1.5 × 0.5 mm base, 0.2 mm high; Fig. 3E). Some layers of small-celled tissue occur on top of the elevations. In a later stage, this tissue is collapsed and nectar is secreted through a dark-coloured depression (Fig. 3F)'.	Blüthgen and Reifenrath (2003)	
Crotalarieae	*Crotalaria* L.	Stem or shoot, inflorescences	AZ	Unknown	Scars of fallen stipules, prophylls, bracts, and flowers (possibly also aborted buds, according to Díaz-Castelazo *et al*. 2005). Undescribed EFNs mentioned to occur near flowers in *C. pallida* (Guimarães *et al*. 2006; Pereira and Trigo 2013). [Note: EFNs reported only in five species in the genus.]	Noack (1903); Zimmermann (1932); Baker *et al*. (1978); Mckey (1989, p. 693); Díaz-Castelazo *et al*. (2005, 2010); Guimarães *et al*. (2006); Melo *et al*. (2010*a*, 2010*b*); Pereira and Trigo (2013)	

Dipterygeae	*Monopteryx* Spruce ex Benth.	Leaves	PA	Elevated	Between the first pair of leaflets.	Barneby and Grimes (1984); this study (observed also on the type specimen of *Monopteryx uaucu* and personal communication and observations by D. Cardoso)	Fig. 15G
Dipterygeae	*Pterodon* Vogel	Leaves	PA	Elevated	On the rachis, located under the insertion of each petiolule, as small elevations whose apical portion is deeply invaginated, resulting in a depression (secretory pore), covered by non-glandular trichomes occurring along the rachis.	Paiva *et al*. (2001)	
Fabeae	*Vicia* L.	Stipules, sepals	TR	Glandular trichomes (exposed)	Concentrated at the base on the abaxial stipule side, often visible by a dark coloured spot; calyx lobes.	Bentley (1977); Baker *et al*. (1978); Pemberton (1990); Endo and Ohashi (1998); Mondor and Addicott (2003); Mondor *et al*. (2006); Heneidak and Hassan (2007); Hernandez *et al*. (2013); Gish *et al*. (2015); this study	Fig. 15J–L
Phaseoleae	*Ancistrotropis* A. Delgado	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011); Gonzalez and Marazzi (2018, as *Vigna peduncularis*)	Fig. 7A
Phaseoleae	*Apios* Fabr.	Inflorescences	AZ	Swollen scar	Secretory abscission of aborted floral buds.	Harvey (2009); this study (based on photograph of inflorescence of *Apios americana*, courtesy of Nicola Patocchi)	Fig. 14A
Phaseoleae	*Bionia* Mart. ex Benth.	Inflorescences	AZ	Swollen scar	Secretory abscission site of aborted floral buds.	Anjos *et al*. (2017); this study (based on field observations of *B. coriacea* and on ant presence at this location in the inflorescence of *Camptosema coriaceum*=*B. coriacea* in the photograph by G. P. Lewis published on p. 397 of Lewis *et al*. 2005)	Fig. 14B, C
Phaseoleae	*Calopogonium* Desv.	Stem or shoot, inflorescences, bracts	AZ	Swollen scar	Well-defined cup-shaped elevations with a central depression that presumably corresponds to the abscission scar of an aborted bud, young bud or bract (Díaz-Castelazo *et al*. 2005, fig. 3B). The location is thus uncertain.	Díaz-Castelazo *et al*. (2005)	
Phaseoleae	*Camptosema* Hook. & Arn.	Inflorescences	AZ	Swollen scar	Secretory abscission site of aborted floral buds.	This study (based on images of *C. ellipticum* specimen by D. Zappi *et al*. 955, on Plants of the world, see http://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30028684-2)	
Phaseoleae	*Canavalia* Adans.	Leaves, inflorescences	AZ	Swollen scar	Peduncles of lateral inflorescences are swollen with multiple secretory scars, i.e. abscission sites of aborted floral buds (Díaz-Castelazo *et al*. 2005, fig. 3C, refer to them as ‘cushions’). Another type of EFN can be found on the developing shoots growing along the stem in the axils of leaves and are similar to the swollen scar found on the inflorescence axis (Díaz-Castelazo *et al*. 2005, fig. 3D).	Zimmermann (1932); Mckey (1989); Koptur (1992*b*); Díaz-Castelazo *et al*. (2004, 2005); Yamashiro and Yamashiro (2008); this study	Fig. 14D
Phaseoleae	*Centrosema* (DC.) Benth.	Inflorescences	AZ	Swollen scar	Swollen and secretory abscission sites of aborted floral buds.	This study (based on field observations of *C. virginianum*)	Fig. 14E

Table 1. (*continued*)

Subfamily and tribe or clade	Genus	Location(s) on plant	Category	Subcategory	Description and notes	Source(s)	Figure(s)
Phaseoleae	*Cleobulia* Mart. ex Benth.	Inflorescences	AZ	Swollen scar	Apparently secretory abscission sites of aborted buds forming a swollen and nectariferous pseudoraceme node. [Note, stipule bases can be reddish and swollen, but have not been observed in this study to be secretory.]	This study (based on field observations of *C. multiflora*)	Fig. 14F
Phaseoleae	*Cochliasanthus* Trev.	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds forming a swollen and nectariferous pseudoraceme node.	Zimmermann (1932, as *Phaseolus caracalla*); Delgado-Salinas *et al*. (2011); this study	Fig. 14G
Phaseoleae	*Condylostylis* Piper	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011); Gonzalez and Marazzi (2018, as *Vigna candida*)	Fig. 7B–D, 14H, I
Phaseoleae	*Cratylia* Mart. ex Benth.	Inflorescences	AZ	Swollen scar	Secretory swollen abscission sites of aborted buds, forming a swollen and nectariferous pseudoraceme node.	This study (based on field observations of *C. mollis*)	Fig. 14J, K
Phaseoleae	*Dioclea* Kunth	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites, forming a swollen and nectariferous pseudoraceme node.	Elias (1983); Blüthgen *et al*. (2000); this study	
Phaseoleae	*Dolichopsis* Hassler	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites, forming a swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011; identification key, p. 1702)	
Phaseoleae	*Dolichos* L.	Leaves, inflorescences	TR, AZ	Glandular trichomes (exposed), swollen scar	Stipels with multicellular trichomes on abaxial side. Swollen secretory abscission sites, forming a swollen and nectariferous pseudoraceme node.	Zimmermann (1932; cites comments by Delpino); this study (based on SEM images of *D. fangitsa* stipels, not shown)	
Phaseoleae	*Erythrina* L.	Stipules, leaves, sepals	TR	Glandular trichomes (sunken)	Multicellular glandular hairs densely packed, mainly on stipule, stipels, and also on petals or sepals, modified calyx lobes. [Note: Sousa-Paiva (2009) reported pericarpic nectaries with postfloral secretion.]	Morini (1886); Zimmermann (1932); Feinsinger *et al*. (1979); Sherbrooke and Scheerens (1979); Lersten and Brubaker (1987); Oliveira and Leitão-Filho (1987); Oliveira and Oliveira-Filho (1991); So (2004); Priest and Loveless (2009); Melo *et al*. (2010*a*, 2010*b*); Carmona-Galindo *et al*. (2014); this study	Fig. 4I–O, 15A, B
Phaseoleae	*Galactia* P.Browne	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Gonzalez and Marazzi (2018)	Fig. 15C
Phaseoleae	*Hardenbergia* Benth.	Stipules, leaves, inflorescences	AZ	Swollen scar	Stipels, stipules, swollen secretory abscission sites of aborted buds.	Lamont (1979); this study (based on ants seen on inflorescence in the photograph by B. D. Schrire in Lewis *et al*. 2005, p. 406)	
Phaseoleae	*Haymondia* A.N.Egan & B.Pan	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Egan and Pan (2015); Egan and Puttock (2016*a*)	
Phaseoleae	*Helicotropis* A.Delgado	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011)	
Phaseoleae	*Kennedia* Vent.	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Marazzi *et al*. (2014)	Fig. 15D, E
Phaseoleae	*Lablab* Adans.	Stipules, leaves, inflorescences	TR; AZ	Glandular trichomes (exposed), swollen scar	On abaxial side of stipules and stipels, exposed glandular trichomes. Swollen secretory abscission sites of aborted buds, easily observed during fruit development.	Zimmermann (1932, citing Delpino); Pemberton (1990; as *Dolichos lablab*); this study (based on many images of infructescences available in Google images)	
Phaseoleae	*Leptospron* (Benth.) A. Delgado	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011)	

Phaseoleae	*Macroptilium* (Benth.) Urb.	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Drewes (1998); Gonzalez and Marazzi (2018); this study	Fig. 7E–G, 15F
Phaseoleae	*Mucuna* Adans. (incl. *Stizolobium)*	Stipules, leaves	TR	Glandular trichomes (exposed)	On stipules and stipels exposed multicellular glandular hairs on abaxial side.	Lersten and Brubaker (1987); Blüthgen and Reifenrath (2003)	
Phaseoleae	*Mysanthus* G.P.Lewis & A.Delgado	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds apparently forming a swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011, fig. 9E); this study	Fig. 15H
Phaseoleae	*Neustanthus* Benth.	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Egan and Pan (2015)	
Phaseoleae	*Oryxis* A.Delgado & G.P. Lewis.	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds forming a swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011, fig. 9F, and identification key on p. 1702)	
Phaseoleae	*Oxyrhynchus* Brandegee	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds forming a swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011; identification key on p. 1702)	
Phaseoleae	*Periandra* Mart. ex Benth.	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds apparently forming a swollen and nectariferous pseudoraceme node.	This study	
Phaseoleae	*Phaseolus* L.	Stipules, leaves, bracteoles	TR	Glandular trichomes (exposed)	Stipules and especially stipels and also bracteoles with an observed nectar droplet bear cluster of exposed glandular trichomes.	Heil (2004); Stenglein (2004); Choh *et al*. (2006); Godschalx *et al*. (2015); Hernandez *et al*. (2013); this study	Fig. 4H, 15I
Phaseoleae	*Physostigma* Balf.	Inflorescences	AZ	Swollen scar	Secretory abscission sites of aborted buds forming a swollen and nectariferous pseudoraceme node.	Zimmermann (1932)	
Phaseoleae	*Pueraria* DC.	Inflorescences	AZ	Swollen scar	Secretory, slightly swollen abscission site of aborted floral buds.	Bentley (1977); Harvey (2009); this study	
Phaseoleae	*Ramirezella* Rose	Inflorescences	AZ	Swollen scar	Secretory and slightly swollen floral nodes modified.	Ochoterena-Booth and Delgado-Salinas (1994)	
Phaseoleae	*Sigmoidotropis* (Piper) A. Delgado	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Delgado-Salinas *et al*. (2011)	
Phaseoleae	*Strophostyles* Elliott	Inflorescences	AZ	Swollen scar	Swollen floral nodes modified into secreting structures.	Riley-Hulting *et al*. (2004); Delgado-Salinas *et al*. (2011)	
Phaseoleae	*Teyleria* Backer	Inflorescences	AZ	Swollen scar	Secretory swollen abscission sites of aborted buds, forming a swollen and nectariferous pseudoraceme node.	Egan and Pan (2015)	
Phaseoleae	*Toxicopueraria* A.N. Egan & B.Pan	Inflorescences	AZ	Swollen scar	Swollen secretory abscission sites of aborted buds.	Egan and Pan (2015); Egan and Puttock (2016*b*, fig. 2)	
Phaseoleae	*Vigna* Savi	Stipules, leaves, inflorescences	TR,AZ	Glandular trichomes (exposed); swollen scar	Stipules and stipels with exposed glandular trichomes on the abaxial side. Secretory swollen abscission sites of aborted buds, forming a swollen and nectariferous pseudoraceme node.	Zimmermann (1932, as *Phaseolus adenanthum*); Kuo and Pate (1985); Delgado-Salinas *et al*. (2011); Aguirre *et al*. (2018); this study	Fig. 4D–G, 7H, I, 15M–P
Phaseoleae	*Wajira* Thulin	Inflorescences	AZ	Swollen scar	Swollen and nectariferous pseudoraceme node.	Thulin *et al*. (2004); Delgado-Salinas *et al*. (2011)	
Robinieae	*Robinia* L.	Stipules, leaves	Unknown	Unknown	On stipules and stipels, but morphological and anatomical description unavailable. [Note: presence reported in the literature, whereas, in this study, EFNs were not detected in repeatedly observed individuals of *Robinia pseudoacacia*.]	Bentley (1977); Pemberton (1990)	

at the Laboratorio de Microscopía y Fotografía de la Diversidad, Instituto de Biología, Universidad Nacional Autónoma de México (Mexico); palladium-sputtered samples were examined and photographed with a Hitachi S-3400 N Type II VPSEM (15 kV) at the University Spectroscopy and Imaging Facilities of the University of Arizona (Arizona, USA).

To illustrate the phylogenetic distribution of EFNs, we mapped the presence of the main categories onto a time-calibrated ultrametric consensus tree derived from the Legume Phylogeny Working Group (2017) *mat*K phylogeny, which includes 710 of the 768 genera, coding genera by category of EFN (and subcategories of parenchymatic EFNs), and, in cases where genera are known to include more than one EFN state, then coding species where known. All optimisations and visualisations were performed in R (ver. 3.5.1, R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org/), using a preliminary time-calibrated version of the Legume Phylogeny Working Group (2017) phylogeny that was inferred with treePL (Smith and O'Meara 2012), using nine fossil calibrations to calibrate internal nodes and 15 secondary calibrations that were derived from a chloroplast exome analysis (E. J. Koenen, unpubl. data) to calibrate the deeper nodes in the family. This chronogram is a preliminary version from a study of macro-evolutionary dynamics in legumes (E. J. Koenen, unpubl. data). Ancestral EFN states were obtained by stochastic character mapping using the make.simmap function of the phytools package (Revell 2012), with an equal-rates model and 200 simulations. Figures were made using various functions of the phytools, ape (Paradis and Schliep 2019) and plotrix (Lemon 2006) packages.

Results and discussion

Ever since the first reports of nectar-producing 'glandulae' (EFNs) in legumes by Hall (1762), the number of legume genera documented as possessing EFNs has steadily increased (Fig. 1). Here, we present the first comprehensively curated list of legume genera with EFNs, detailing their systematic and phylogenetic distribution (Tables 1, 2, Fig. 2), locations on the plant (Table 3, Fig. 3), morphology and anatomy (including proposing a revised and unified classification of EFN categories; Table 4, Fig. 4–7), all of this amply illustrated with 111 images covering taxa in all four legume subfamilies with EFNs (Fig. 8–15). We confirm the presence of EFNs in 153 genera, i.e. 20% of total legume genera, distributed across the following four subfamilies (Tables 1, 2), in a systematic order: Cercidoideae (1 genus), Detarioideae (19 genera), Caesalpinioideae (87) and Papilionoideae (46). Of the six subfamilies, Caesalpinioideae has the highest proportion of genera with EFNs, with ~60%, followed by Detarioideae and Papilionoideae, with 23 and 9% respectively (Table 2). We could find no reports or evidence for EFNs in subfamilies Dialioideae and Duparquetioideae. Reports from 43 genera remain unclear or lack sufficient reliable detail to confirm the mentioned structures as EFNs (Table S1, available as Supplementary material to this paper), in line with doubts expressed by previous authors (e.g. Mckey 1989; Koptur 1992*a*). Although, we found explicit reports of absence of EFNs for 36 genera (Table S2 in the Supplementary material), it was beyond the scope of this study to verify these. In the following sections, we present an overview of the diversity of locations, morphology and anatomy of EFNs, discuss this diversity and relevant ecological information for each subfamily and, finally, outline preliminary ideas on the evolutionary history of EFNs within Leguminosae and future research priorities.

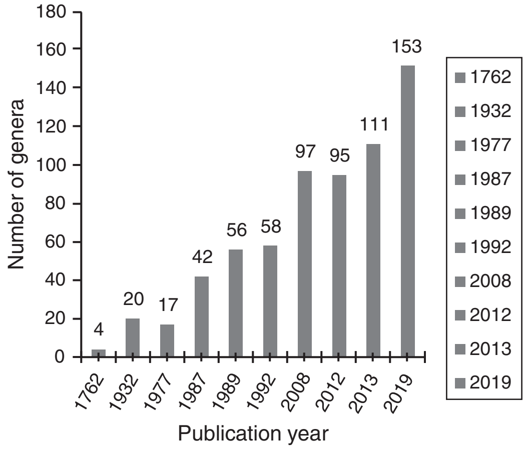

Fig. 1. Number of extrafloral nectary-bearing legume genera reported in the literature. Selected reviews in the order of publication year: Hall (1762), Zimmermann (1932), Bentley (1977), Lersten and Brubaker (1987), Mckey (1989), Koptur (1992*a*), Keeler's online world list of plants with extrafloral nectaries (EFNs; original list, Keeler 2009; replaced by Weber *et al*. 2015), Marazzi *et al*. (2012), Weber and Keeler (2013), and the present study (2019).

Diversity in location, morphology and anatomy

Leguminosae is one of the most, if not *the* most, diverse plant family in terms of the location of EFNs on a plant, i.e. the organs that bear EFNs, and in terms of EFN morphology and anatomy. Although here presented separately, EFN location, morphology and anatomy are closely connected, because the development, ecology and evolution of EFNs ultimately depend, at least to some degree, on that of its bearing organ (Marazzi *et al*. 2013*a*; see also below, section 'Legume EFNs: a phylogenetic and evolutionary perspective').

Location of EFNs

The locations of nectaries on plants have long been used to distinguish extrafloral from floral nectaries (Caspary 1848), well before their functional significance and very different ecological roles were recognised (Delpino 1868, 1869, 1870, 1873, 1874)[2]. EFN locations can be divided into vegetative and reproductive (i.e. extra-reproductive *v.* reproductive *sensu* Schmid 1988), given their different protective functions for developing shoots and leaves *v.* developing flowers (buds) and fruits

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[2] According to Schmid (1988), the part on nectaries appears in Delpino (1873, pp. 233–275 and, although dated 1873, apparently was issued 1874. The entire work was issued as a separate publication in 1875, with new pagination, Abstracts in *Botanische Zeitung* vol. 29, pp. 443–445, 447–459, 463–467, vol. 33, p. 807 and Just's *Botanischer Jahresbericht* vol. 2, pp. 881–896, the last by Hermann Müller.

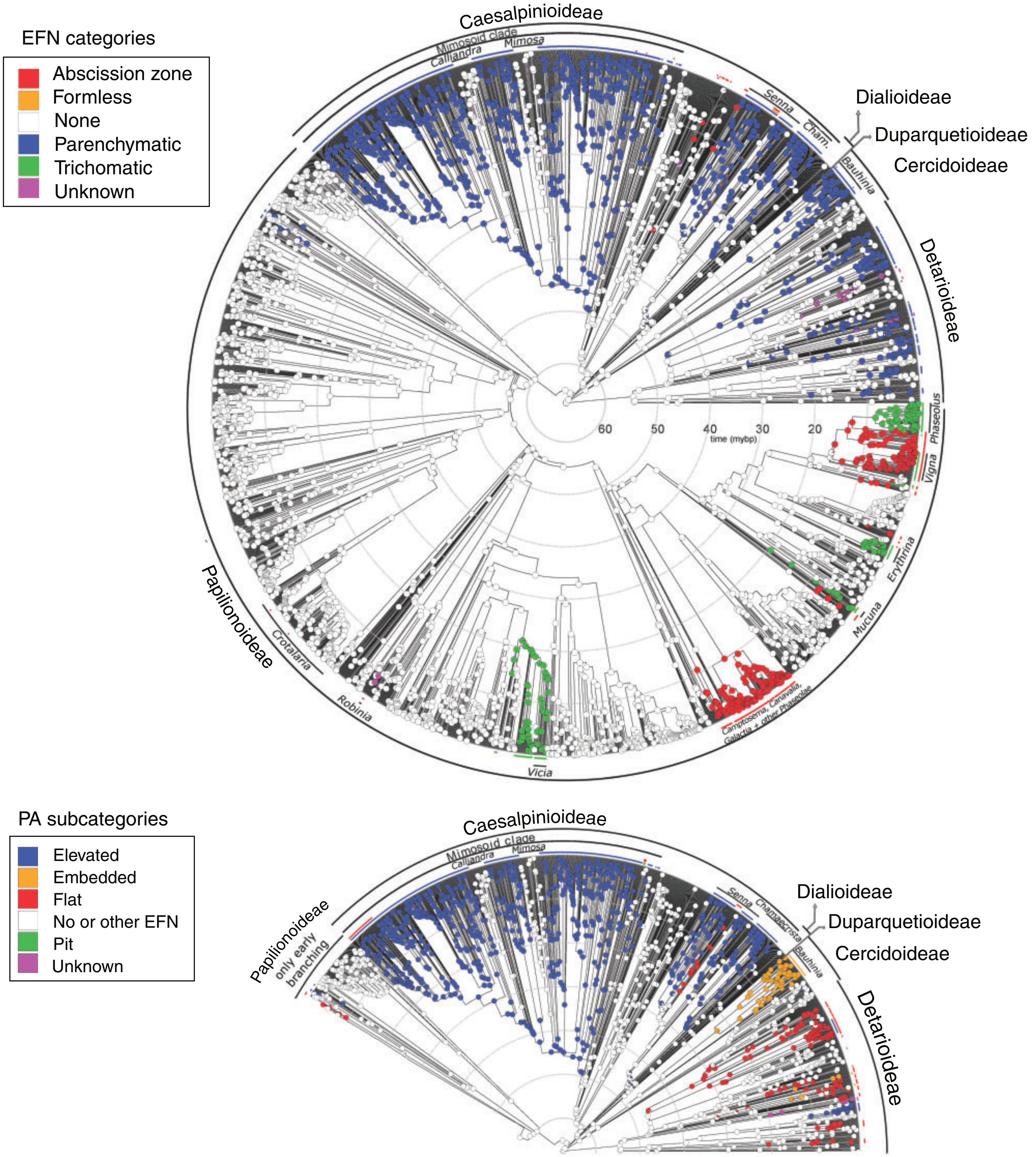

Fig. 2. Phylogenetic distribution of extrafloral nectaries (EFNs) in Leguminosae. Phylogenetic distribution of the main EFN categories and subcategories of the parenchymatic category (PA; only relevant part of the tree shown) mapped by stochastic character mapping onto a time-calibrated ultrametric consensus tree (E. J. Koenen, unpubl. data) derived from the Legume Phylogeny Working Group (2017) *mat*K phylogeny of Leguminosae. Subfamilies plus selected clades and genera are indicated. Grey circles indicate the timescale.

respectively. In Leguminosae, we identify the following nine different EFN locations (Table 3, Fig. 3): (1) shoots and stems, (2) stipules, (3) between stipules (intrastipular), (4) leaves, (5) inflorescence axes, (6) pedicels, (7) bracts, (8) bracteoles and (9) sepals. Furthermore, the exact position can vary on single organs; for example, stipule EFNs can occur on the lobe or on the abaxial lamina side, or in bracts, they can be on the bract petiole or on the dorsal lamina side. Variation is particularly outstanding in leaves of legumes, because EFNs can occur on many different parts of the compound leaves (pinnate or bipinnate), including (1) the

Table 2. Phylogenetic distribution of genera with extrafloral nectaries (EFNs) in subfamilies of the Leguminosae

Numbers of genera are based on Table 1; numbers for the Mimosoid clade nested within Caesalpinioideae are also indicated. Total number of genera is based on Legume Phylogeny Working Group (2017). Note that no genera with EFNs are known from the other two subfamilies Dialioideae and Duparquetioideae

Taxon	Number of confirmed genera	Number of total genera	Proportion within family or subfamily (%)	Proportion of all genera with EFNs (%)
Leguminosae	153	765	20.0	–
Cercidoideae	1	12	8.3	0.7
Detarioideae	19	84	22.6	12.4
Caesalpinioideae	87	148	58.8	56.9
Mimosoid clade	78	87	89.7	51.0
Papilionoideae	46	503	9.1	30.1

Table 3. Locations of extrafloral nectaries (EFNs) across Leguminosae and subfamilies

Numbers of genera are based on Table 1. The description 'leaf rachis' means between leaflets, on a pinna rachis, and between pinnae. Dashes indicate absence of that location. Question marks denote a reliable report that remains to be confirmed

Location description	Leguminosae	%	Cercidoideae	Detarioideae	Caesalpinioideae	Papilionoideae
Vegetative only	98	64.1	–	17	77	4
Reproductive only	33	21.6	–	–	2	31
Vegetative + reproductive	22	14.4	1	2	8	11
(1) Vegetative total	119	77.8	1	19	85	14
Stem or shoot	10	6.5	–	1	6	3
Stipules	14	9.2	–	2	4	8
Intrastipular structure	1	0.7	1	–	–	–
Leaves	114	74.5	1	18	82	13
Petiole	52	45.6	–	–	51	1
Leaf lamina	15	13.2	–	15	–	–
Leaf margin	3	2.6	–	3	–	–
Leaf rachis	71	62.3	1?	–	69	2
Leaf stipels	10	8.8	–	–	–	10
Leaf rachis tip	4	3.5	–	–	4	–
Leaf unspecified	1	0.9	–	–	–	1
(2) Reproductive total	55	35.9	1	2	10	42
Inflorescence axes	40	26.1	–	–	2	38
Abscission zone (bud)	37	92.5	–	–	–	37
Abscission zone (bract)	3	7.5	–	–	2	1
Unknown	1	2.5	–	–	–	1
Pedicels	2	1.3	–	–	2	–
Bracts	9	5.9	–	2	5	2
Bracteoles	3	2.0	1	1	–	1
Sepals	2	1.3	–	–	1	1
Number of locations						
One	125	81.7	–	16	77	32
Two	17	11.1	–	2	6	9
Three	8	5.2	–	–	2	6
Four	3	2.0	1	1	1	–
Five	1	0.7	–	–	1	–

petiole (Fig. 10D–E, P), (2) along the primary and secondary (for bipinnate leaves) rachises between the pairs of leaflets or pinnae (Fig. 10F), including at the apex of the rachis (Fig. 10D), and (3) on the mucro (apparently only in *Senna scabriuscula*), together with a petiole EFN (Fig. 10N), (4) on stipels (usually the abaxial side), (5) on the leaflet lamina (usually the abaxial side, Fig. 9A–D) and (6) on leaflet margins (Fig. 9E, J, K). Schmid (1988)'s topographical classification of nectaries lacks some of these leaf locations, probably because he only considered simple leaves. EFNs located on the abscission zones of abortive buds or caducous bracts are here referred to inflorescence axes because they are more accurate than locating them on the abscised organs themselves. These assignments of EFNs to specific plant locations allow us to identify patterns in the frequencies of EFNs across different plant parts.

Extrafloral nectaries are not equally distributed across locations. In the majority of genera (nearly 80%), EFNs apparently are found at a single location, and, more generally, on vegetative parts (64%) only, whereas fewer bear them on reproductive parts only or on both parts (20.9 and 14.4%

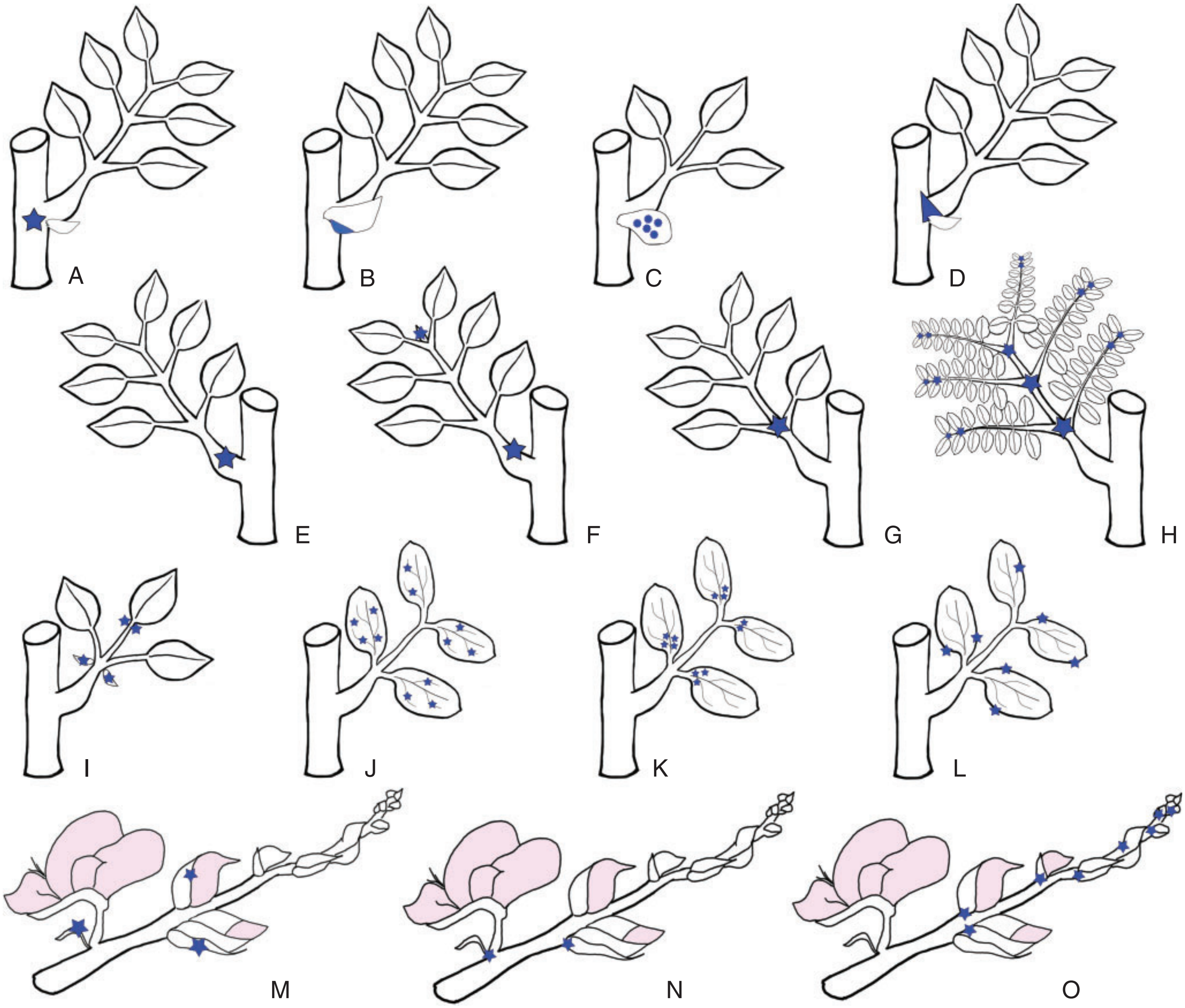

Fig. 3. Diversity of locations of extrafloral nectaries (EFNs) in Leguminosae. Stars and dots indicate representative locations, including examples of the variation in the position of EFNs on individual organs bearing them. A. Stems and shoots. B. Stipule lobe. C. Stipule lamina (abaxial surface). D. Between stipules (intrastipular). E. Petiole (at variable positions from base to apex). F. Petiole and mucro. G, H. Variably between pairs of leaflets and pinnae. G. Between first pair only. H. Between some or all pairs (on bipinnate leaves: EFNs on some of the pinnae rachises, often EFNs at the tips of pinnae). I. Stipels. J, K. Leaflet lamina (abaxial surface). L. Leaflet margin. M–O. Inflorescences. M. Bract petiole, bract dorsal side, and sepal dorsal side. N. Abscission zones of bracts. O. Abscission zones of pedicels (e.g. abortive buds or falling flowers).

respectively; Table 3). However, it is possible that EFNs in a few genera (especially Caesalpinioideae) also develop on leaves that subtend inflorescences but these have been reported simply as leaves, instead of inflorescence bracts. The 27 genera with EFNs at multiple locations are scattered across legumes, but the caesalpinioid genus *Senna* is outstanding, with EFNs at up to five different locations across the genus as a whole, although individual plants bear EFNs in up to two to three locations at most (depending on the species and clade; Marazzi *et al*. 2013*b*). Beyond these trends, specific locations of EFNs are, in general, associated with particular clades; intrastipular EFNs are characteristic of subfamily Cercidoideae (*Bauhinia*), leaflet-lamina and leaflet-margin EFNs occur exclusively in subfamily Detarioideae, EFNs on inflorescence axes and stipels are, with a few exceptions, restricted to subclades of Papilionoideae, whereas EFNs on the petiole and the leaf rachis are prevalent in Caesalpinioideae. However, patterns in the evolution of EFN diversity can be correctly interpreted only when considering location alongside morphology and anatomy.

Morphological and anatomical categories and terminology of EFNs

Review of the legume anatomical literature shows a broad range of terms used to describe and categorise EFNs in different studies and different taxonomic groups. Given this

Table 4. Categories of extrafloral nectaries (EFNs) across Leguminosae subfamilies
Numbers of genera are based on Table 1. Dash indicates absence of that category or subcategory

Category and subcategory	Figure number	Leguminosae	Cercidoideae	Detarioideae	Caesalpinioideae	Papilionoideae
Formless (FO)	4A–C	1	–	–	1	–
Trichomatic (TR)		6	–	–	–	6
Exposed (ex)	4E–H	5	–	–	–	5
Hollow (ho)	4I–O	1	–	–	–	1
Parenchymatic (PA)		105	2	20	86	4
Embedded (em)	5A–F	3	1	2	–	–
Pit	5G	1	–	–	1	–
Flat (fl)	5H–O	19	–	14	3	2
Elevated (ev)	6	85	–	2	81	2
Unknown		4	1	2	2	–
Abscission zone (AZ)		42	–	–	5	37
Non-differentiated (nd)	10B, C, L	5	–	–	5	–
Swollen-scar (ss)	7	36	–	–	–	36
Unknown		1	–	–	–	1
Unknown category		3	–	1	1	1
Multiple categories		8	1	1	3	3

terminological disparity, we propose a revised classification of EFN types and a unified and standardised terminology for EFNs that builds on the two most widely used existing classifications of Zimmermann (1932) and Elias (1983). One previous study attempting a classification was by Ono (1907).

Extrafloral nectaries can be fundamentally divided into two main groups, namely, non-structural and structural. The first represents the *gestaltlose Nektarien* of Zimmermann (1932), equivalent to the ‘formless’ EFNs of Elias (1983). These lack any specifically differentiated nectariferous structure, meaning that nectar is secreted from tissues without any structural specialisation at the tissue or organ level (Wettstein 1889; Zimmermann 1932; Elias 1983; Bernardello 2007).

Formless EFNs are one of the most overlooked types of EFN in angiosperms (Bernardello 2007), including legumes, because they can be detected and located only on the basis of observations of the presence of droplets of nectar or presence of ants. For instance, in this study, we confirmed the occurrence of this EFN category only in the caesalpinioid genus *Senna* (Table 1, Fig. 4A–C), on the basis of studies by Marazzi *et al.* (2013*b*) who observed nectar secretion on the dorsal surfaces of bracts and sepals in species of *Senna* Clade II; however, detailed anatomical studies did not find any nectariferous structure or tissue associated with the nectar secretion (data not shown).

In structural EFNs, the nectary is recognised by the presence of specialised nectar-producing and -secreting tissues. In general, nectaries (both floral and extrafloral) conform to the structure proposed by Nepi (2007), comprising a nectary epidermis (that mediates nectar release to the outside), nectary parenchyma (directly involved in nectar production and secretion) and subnectary parenchyma (tissue related to nectar production). Structural EFNs may or may not be vascularised, and the vascular supply can be specific to the nectary itself or derived from that of the nearest vascular system. Several distinct types of structural EFNs can be recognised.

First, nectar producing multicellular glandular trichomes are here designated as trichomatic EFNs. In most cases, such trichomes are aggregated, forming a secretory unit that is visible as an EFN. Zimmermann (1932) and Elias (1983) did not recognise this category, whereas Vogel (1977) did (calling it’trichomatous’ EFNs). Trichomatic EFNs are found in at least six legume genera (Table 4). These trichomatic EFNs can be divided into two subcategories, namely, exposed (simply lined on the organ surface) and hollow (sunken into a depression or cavity), the latter corresponding to the ‘*Hohlnektarien*’ of Zimmermann (1932), and equivalent to the ‘hollow’ nectaries of Elias (1983). For the few legume genera with trichomatic EFNs, most have exposed trichomatic EFNs (*Lablab*, *Mucuna*, *Phaseolus*, *Vicia* and *Vigna*; Table 1, Fig. 4E–H, 15M, N). These comprise nectariferous patches of densely packed clavate trichomes on the abaxial side of auriculate stipules, stipels and bracteoles, forming an irregular or triangular to circular surface (1–3 mm in diameter in the species studied) lacking stomata. However, in at least one species of *Mucuna*, the trichomes are sparsely distributed on the filiform stipels (Lersten and Brubaker 1987). According to Ono (1907), *Vicia* was the first genus to be studied anatomically (Fuckel 1846). Hollow trichomatic EFNs have been found within legumes, only in the genus *Erythrina*, on stipels and calyx lobes (Table 1, Fig. 4I–O). In this case, the trichomes themselves are barely visible externally, the stipels and calyx lobes appear swollen, and are structurally modified by the EFN (Fig. 15A, B).

The majority of structural EFNs are parenchymatic, meaning that they are characterised by the presence of secretory tissue formed by small, densely packed thin-walled cells, with a dense and glandular cytoplasm. In these EFNs, the epidermis is the tissue through which nectar exudes; therefore, it is of glandular nature and lacks stomata or secretory trichomes. Parenchymatic EFNs encompass the remaining five types of Elias (1983, based on Zimmermann 1932), namely, ‘embedded’, ‘pit’, ‘flattened’, ‘elevated’ and ‘scale-like’. We follow this classification, modifying it only slightly, and found all of these types of parenchymatic EFNs in legumes (Table 4), except for scale-like EFNs, which are not known to occur.

In embedded EFNs, the secretory cells are completely embedded in the tissue of the organ bearing the EFN, with a

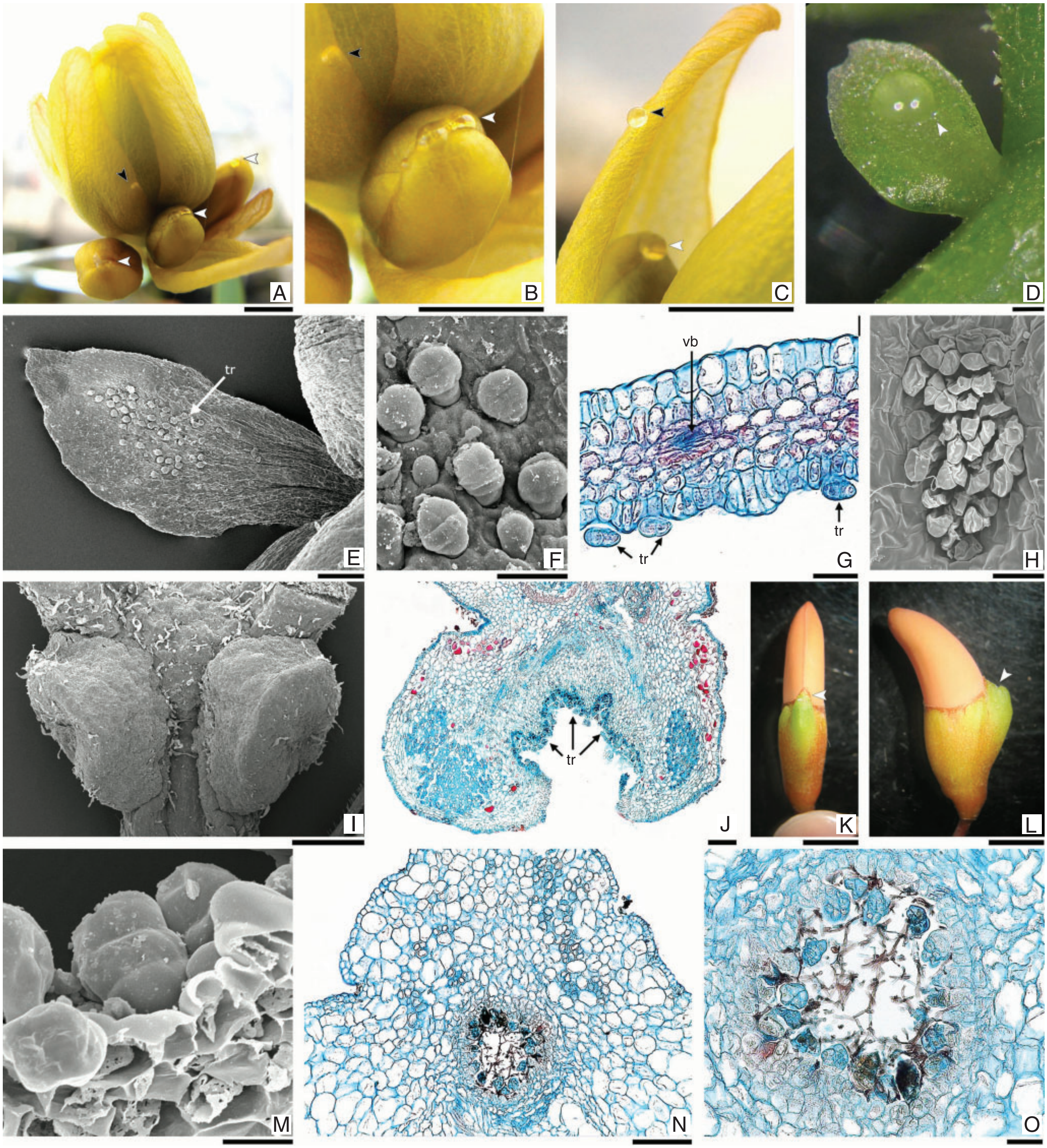

Fig. 4. Categories of extrafloral nectaries (EFNs) in Leguminosae: formless and trichomatic EFNs. A–C. Formless EFNs on flowers of *Senna pleurocarpa*, Caesalpinioideae; black and white arrowheads indicate nectar drop on sepals and bracts respectively. D–G. Exposed trichomatic EFNs in *Vigna unguiculata*, Papilionoideae. D. Stipel with nectar drops. E, F. Scanning electron micrographs (SEMs) of glandular trichomes on stipels. G. Transverse section (TS) of stipel in EFN area, glandular trichomes on adaxial epidermis. H. SEM of exposed trichomatic EFNs of stipels in *Phaseolus lunatus*, Papilionoideae (herbarium material). I–O. Hollow trichromatic EFNs. I, J. Hollow trichromatic EFNs in *Erythrina crista-galli*, Papilionoideae. I. SEM of swollen stipels modified into EFNs. J. Longitudinal section of stipel, showing the glandular trichomes. K–O. Hollow trichromatic EFNs on calyx lobe of *Erythrina dominguezii*. K, L. Dorsal and lateral view of flower; arrow heads indicate EFNs. M. SEM of glandular trichomes. N, O. TS of calyx lobe, showing the glandular trichomes lined within the cavity. N. Note the presence of black fungal hyphae over the trichomes. tr, trichomes; vb, vascular bundles. Scale bars: 0.5 cm (A–C, K, L); 1 mm (D); 200 µm (E, I, J, N); 50 µm (F–H, O); and 20 µm (M).

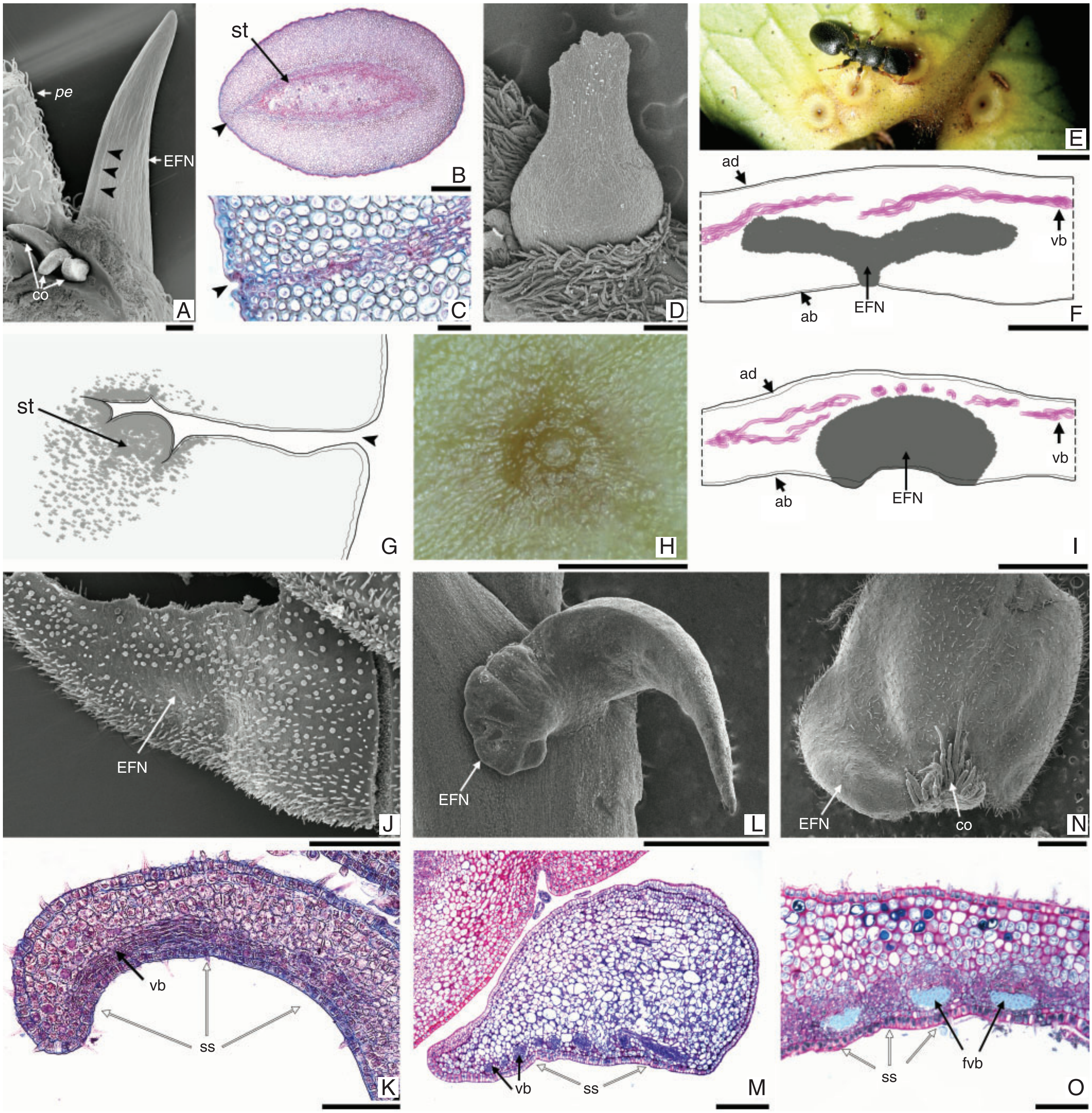

Fig. 5. Categories of extrafloral nectaries (EFNs) in Leguminosae: embedded, pit and flat EFNs. A–C. *Bauhinia forficata* subsp. *pruinosa*, Cercidoideae; arrowheads indicate groove for nectar release. A. Scanning electron micrograph (SEM) of secretory prickles (EFN). B. Transverse section (TS) of prickle-EFN showing embedded secretory tissue. C. Detail of the secretory zone reaching the prickle surface and ending with a small groove. D. SEM of *Bauhinia macranthera*, intrastipular EFN. E–F. Embedded EFNs of *Leonardoxa africana*, Detarioideae. E. Adaxial leaflet surface showing three EFNs. F. Diagram of leaf section, based on fig. 3 of Elias (1980). G. Diagram of pit EFN of *Entada phaseoloides*, Caesalpinioideae, Mimosoid clade, based on fig. 3C of Blüthgen and Reifenrath (2003). Arrowhead indicates location of nectar release. H. Flat EFNs of *Cynometra ramiflora*, Detarioideae. I. Diagram of flat EFN of *Humboldtia brunonis*, Detarioideae, based on fig. S2 of Chanam *et al*. (2015). J–O. Flat EFNs on stipules of *Senna* species, Caesalpinioideae, SEM and TS. J, K. *S. alata*. L, M. *S. pleurocarpa*. N, O. *S. martiana*. ab, abaxial epidermis; ad, adaxial epidermis; co, colleters; fvb, fibres and vascular bundles; pe, petiole; ss, secretory surface; st, secretory tissue; vb, vascular bundles. Scale bars: 1 mm (E, L, N); 0.5 mm (H, J); 200 µm (A, B, D, F, I); 50 µm (k, o, m); and 20 µm (c). Section stains: safranin–astra blue (B–C, K); ruthenium red–toluidine blue (M, O). Photos: Rumsaïs Blatrix (F); Aleksandar Radosavljevic (H).

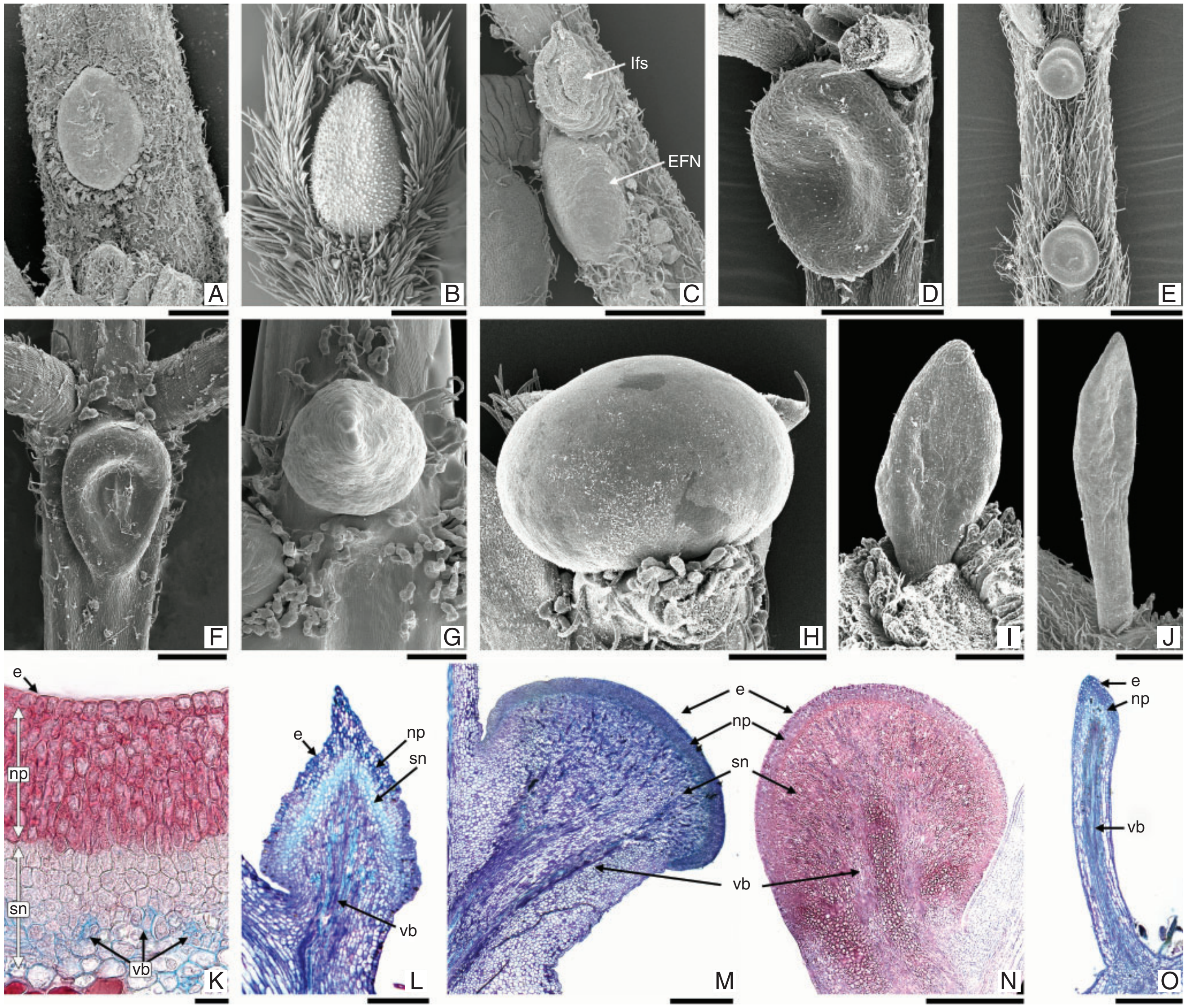

Fig. 6. Categories of extrafloral nectaries (EFNs) in Leguminosae: elevated EFNs. A–J. Scanning electron micrographs (SEMs) of elevated EFNs (all Caesalpinioideae). A. *Lysiloma divaricatum*, petiole. B. *Senna mucronifera*, early stage leaf. C. *Enterolobium contortisiliquum*, pinnular rachis (one leaflet removed). D. *Desmanthus acuminatus*, petiole. E. *Chamaecrista* cf. *nictitans*, petiole. F. *Leucaena leucocephala*, rachis. G. *Senna septemtrionalis*, rachis. H. *Senna scabriuscula*, bract. I, J. *Senna tonduzii*, base of pedicels. K–O. Longitudinal sections of EFN. K. Detail of EFN anatomy in *Desmanthus acuminatus.* L. *Senna morongii*, rachis. M. *S. occidentalis*, petiole. N. *S. scabriuscula.* O. *S. odorata*. e, epidermis; lfs, leaflets; np, nectary parenchyma; sn, subnectary parenchyma; and vb, vascular bundles. Scale bars: 0.5 mm (A–H, J, N, O), 200 µm (I, L, M) and 20 µm (K). Section stains: safranin–astra blue (K, N); ruthenium red–toluidine blue (L, M, O).

minimal area reaching the surface to release nectar. Embedded EFNs occur in only three legume genera (Table 4), namely, *Bauhinia* (Cercidoideae) and two Detarioideae, *Leonardoxa* and *Plagiosiphon*. In *Bauhinia*, they are intrastipular secretory structures or secretory prickles (Fig. 5A–D). Anatomically, the secretory tissue is inside the prickle, between the parenchyma and the cortex, and extends to the prickle epidermis, and, in this way, the EFNs appear like one-sided spindles (Gonzalez and Marazzi 2018). In the two detarioids, the EFNs are on the abaxial side of the leaflet lamina, embedded in the mesophyll (Fig. 5E, F; Elias 1980; Mckey 1989).

Pit EFNs are sunken in the tissues of other organs, and the ‘depressions in which they lie are usually steep-sided and have a diameter that equals or exceeds that of the nectaries’ (Elias 1983, p. 177). In Leguminosae, pit EFNs occur apparently in only one genus, the mimosoid *Entada* (Table 1; reported as such by Blüthgen and Reifenrath 2003; Fig. 5G). *Entada* pit EFNs lack glandular trichomes. However, it should be noted that many of the pit nectaries mentioned by Zimmermann (1932) as ‘*Grubennektarien*’ do have trichomes; for clarity, we suggest restricting the use of the ‘pit’ EFN category to those nectar-secreting cavities lacking trichomes.

Flat EFNs correspond to Elias’ ‘flattened’ EFNs (‘*Flachnektarien*’ of Zimmermann 1932). Here, it is important to bear in mind that ‘flat’ should not be confused with ‘flattened’, which is widely used to describe EFN shapes of, for example,

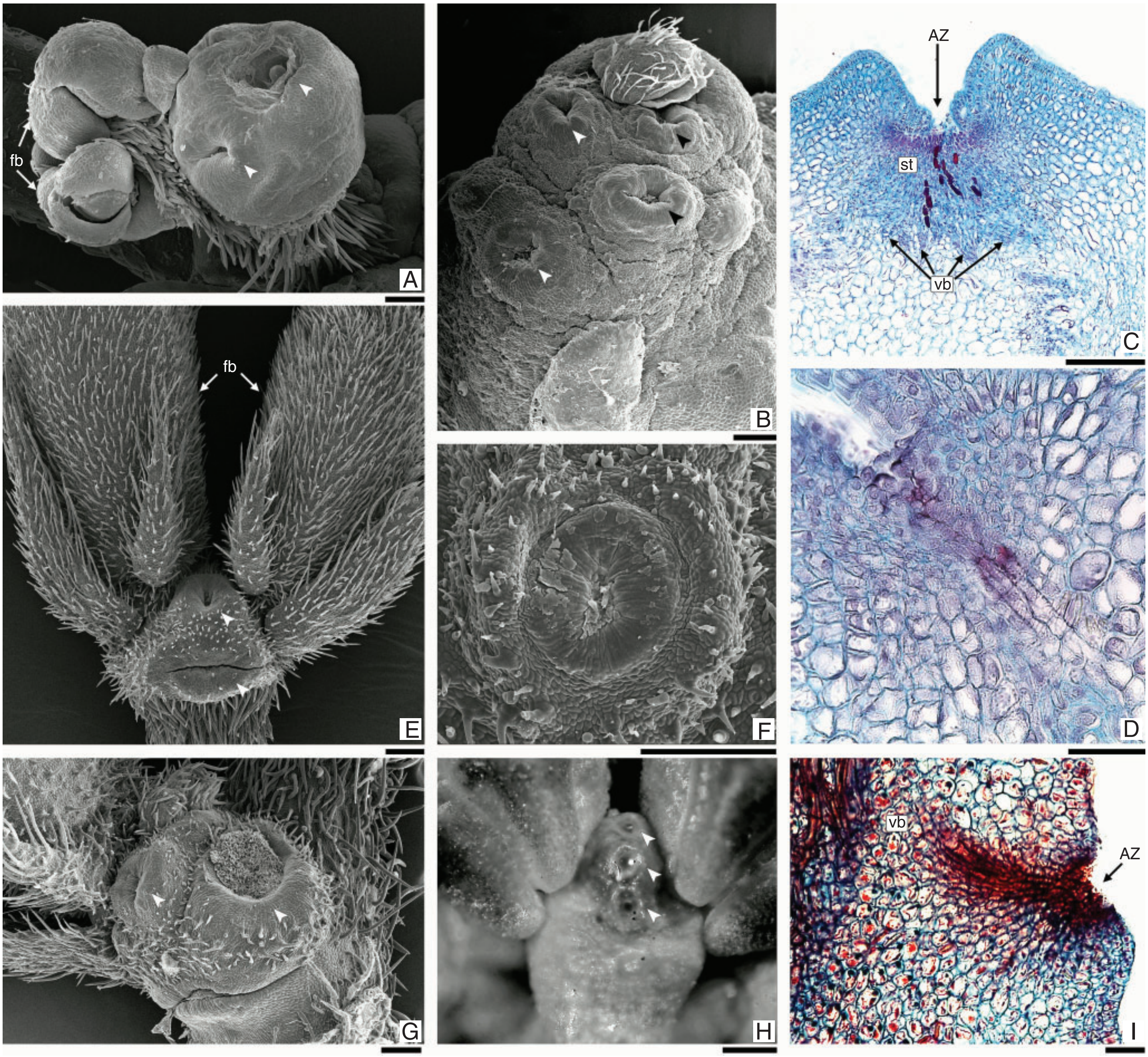

Fig. 7. Categories of extrafloral nectaries (EFNs) in Leguminosae: Abscission-zone EFNs. Arrowheads indicate positions of abscission-zone (AZ) EFNs on inflorescence axis (all Papilionoideae). A. *Ancistrotropis peduncularis*. B–D. *Condylostylis candida*. B. Scanning electron micrograph (SEM). C, D. Longitudinal sections (LS) through swollen-scar EFN. E. *Macroptilium prostratum*. F, G. *Macroptilium gibbosifolium.* H, I. *Vigna unguiculata*. H. Apical inflorescence axis. I. LS. fb, floral bud; st, secretory tissue; and vb, vascular bundles. Scale bars: 1 mm (H), 200 µm (A–C, E–G) and 50 µm (D, I). Section stains: all safranin–astra blue.

elevated nectaries. The secretory surface of flat EFNs is at the level of the organ-bearing tissue (Fig. 5J–O). In legumes, flat EFNs occur in 19 genera (Table 4), on stipule lobes where they are visible as a coloured area (*Senna*, Fig. 10K), on leaves (*Acacia s.str*.), on twig junctions and bracts (*Entada*) or bracts only (*Alexa*), scattered over the stem, rachis and leaflets (*Castanospermum*; Table 1), and on the abaxial surfaces of leaflets (14 genera of detarioids), where they are visible as tiny circular structures with a flattened, slightly concave or convex surface, generally no larger than 1 mm in diameter (Fig. 9). Hawthorne and Jongkind (2006) referred to these detarioid flat EFNs as 'knotted vein glands', probably because the leaflet secondary veins are often radially arrayed around the EFN (but separated from the nectary parenchyma), a pattern described as stellate by de la Estrella *et al*. (2012). These flat detarioid EFNs are within the foliar mesophyll, with the nectary parenchyma being located between the vascular tissues and the epidermis, and the secretory surface of the EFN is formed by an epidermis and nectar accumulates under the cuticle (Paiva and Machado 2006; Melo *et al*. 2010*b*; Chanam *et al*. 2015). They can also be noticed as a bulge on the adaxial leaflet surface.

Fig. 8. Diversity of extrafloral nectaries (EFNs) in Cercidoideae. Arrowheads indicate positions of EFNs. A, B. *Bauhinia corniculata*. A. Ant collecting nectar from EFN. B. Intrastipular EFN. C, D. *Bauhinia forficata* subsp. *pruinosa*. D. Node showing secretory prickles with nectar drop. E–F. *Bauhinia macranthe*ra var. *grayana*. G, H. *Bauhinia variegata*; nectar drops lateral to bracteoles;nunknown EFNs. br, bracteoles; bu, bud; ls, leaf scar; nd, nectar drop; sp, secretory prickles; and st, stipules.

Elevated EFNs (or '*Hochnektarien*', Zimmermann 1932) are more or less protruding from the organ that bears them (Fig. 6, 11–13). They are the most common category of EFN in legumes, present in 85 genera (55% of all EFN-bearing genera), of which only four are outside the Caesalpinioideae (Table 4). These EFNs are most often associated with leaves, where they occur at many different positions on the petiole, leaf rachis and secondary rachises of bipinnate leaves (see also Table 3). They are larger in size than all other categories of EFN and usually easily visible on herbarium material; hence, they have often been used as taxonomic characters. They are also extremely diverse in shape, being sessile, cupuliform or stalked, elongated or rounded, their surfaces concave or convex (Fig. 6A–J). Their anatomical organisation (shared with flat EFNs) is more constant, comprising a secretory epidermis, nectary parenchyma and subnectary parenchyma that is often served by vascular bundles derived from the nearest vascular system (Fig. 6K–O). In the elevated EFNs of *Senna*, there is an additional layer of meristematic cells between the nectary and the subnectary parenchyma (Marazzi *et al*. 2013*b*; Gonzalez and Marazzi 2018). EFNs in the detarioid genera *Gilbertiodendron* and *Copaifera* are slightly elevated, located on leaflet margins, and are reminiscent of (and possibly a transitional form to) the flat EFNs typical of Detarioideae, but they are protruding from the leaflet margins (as opposed to the lamina where most detarioid EFNs are found), and are hence best categorised as elevated EFNs.

The last category, here designated as abscission-zone EFNs, are modifications of the insertion region of organs, mainly in the inflorescence, such as pedicels and bracts, but also of stipules. Two subcategories can be recognised, namely, non-differentiated abscission zones (found only in 5 caesalpinioid genera) and differentiated swollen scars (in 36 papilionoid genera, restricted to tribe Phaseoleae; Tables 1, 3, Fig. 7). In most non-differentiated abscission-zone EFNs, the flowers develop normally but the subtending bract may fall early and nectar is released through the groove that marks the separation zone, delimiting the abscission zone between the pedicel and the inflorescence axis (in *Caesalpinia s.str*. (Fig. 10B, C), *Gelrebia*, *Libidibia*, and *Senna* (Fig. 10J)). Such a nectary can also occur in the abscission zone of stipules (in *Caesalpinia s.str.* and *Pseudoprosopis*). These EFNs lack differentiated nectariferous tissue, but because nectar release is associated with an abscission zone, we do not consider them to be formless EFNs. Like formless EFNs, they are also probably largely overlooked, because only the presence of nectar or ants allows their detection. The second subcategory of abscission-zone EFNs, swollen-scar EFNs, are always associated with abortion of flower buds (Fig. 7, 14). After flower abortion, instead of simply forming a typical abscission-scar zone, a complex, volcano-shaped structure develops consisting of a central depressed area, with a mix of secretory cells and the pre-existing vascular supply, and a marginal swollen area, lacking obvious secretory features (Fig. 7). For a detailed discussion of this type of nectary, see Gonzalez and Marazzi (2018, and references therein).

Finally, reviewing the legume anatomical literature also shows a miscellany of other secretory structures that have been reported as EFNs, possibly because they were called 'glands' (see Tables S1, S2, available as Supplementary material to this paper), but which do not fulfill the required criteria for an EFN. 'Gland' is a very general term, used to

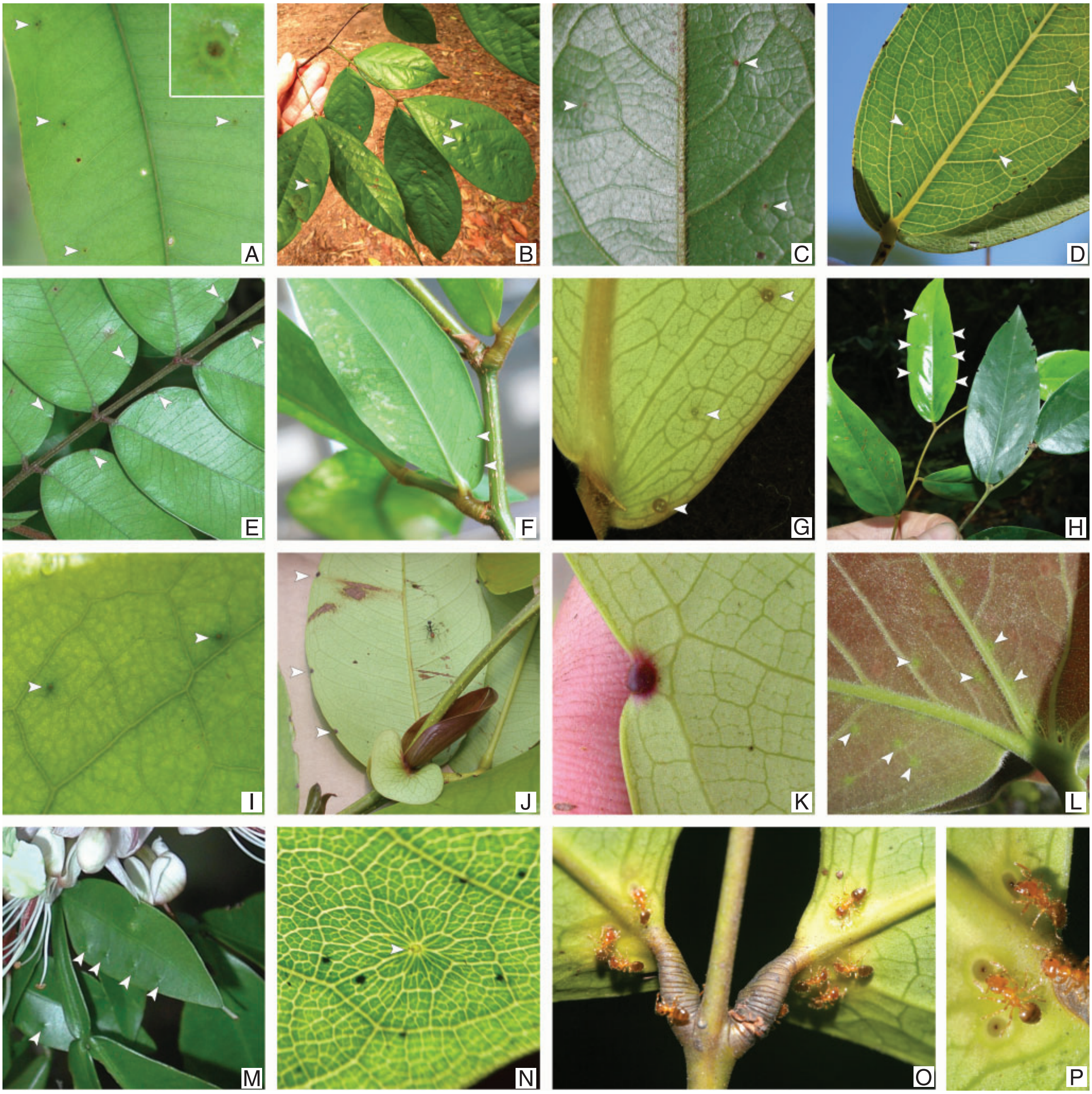

Fig. 9. Diversity of extrafloral nectaries (EFNs) in Detarioideae. All EFNs are parenchymatic. Arrowheads indicate positions of EFNs. On leaflet lamina, adaxial surface (B, D, H, M) orabaxial surface (A, C, F, G, I–L, N–P) or leaflet margin (E, J, K). A. *Afzelia africana*, box showing close up of flat EFN. B, C. *Anthonotha vignei*, flat. D. *Brachystegia bussei*, flat. E. *Copaifera salikounda*, elevated. F, G. *Cynometra ramiflora*, flat. H, I. *Didelotia idae*, flat. J, K. *Gilbertiodendron splendidum*, elevated. L. *Hymenaea* sp. indet., flat. M. *Hymenostegia afzelii*, flat. N. *Isomacrolobium elongatum*, flat. O, P. *Leonardoxa africana*, flat. Photos: Rumsaïs Blatrix (O, P), William Hawthorne (B–E, H–K, M, N) and Aleksandar Radosavljevic (F, G).

indicate any secretory structure, and has been used to refer to both true EFNs, but also to other secretory structures, notably glandular trichomes (non-nectar secreting or of unknown secretion) and colleters (i.e. secretory emergences producing sticky mixtures of mucilage and terpenes). For example, the presence of glandular trichomes distributed throughout the plant and erroneously interpreted as EFNs were described in *Rhynchosia minima*, Papilionoideae (Bhattacharyya and Maheshwari 1970; Khan *et al.* 2017), and *Poincianella bracteosa* (now *Cenostigma bracteosum*, see Gagnon *et al.* 2016), Caesalpinioideae (Melo *et al.* 2010*a*, 2010*b*). The capitate trichomes in the caesalpinioid genus *Hoffmannseggia* and in *Erythrostemon gillesii* were described as ‘glands’ and considered as EFNs by authorities like Delpino (1886, 1887,

1889) and Zimmermann (1932), but we consider these reports to be doubtfully true EFNs in line with Mckey (1989). More examples of this sort of confusion with other secretory structures are elaborated in the following sections on each subfamily.

Cercidoideae

Of the 12 genera in subfamily Cercidoideae (formerly placed in the more broadly circumscribed Caesalpinioideae, Legume Phylogeny Working Group 2017), only *Bauhinia* appears to include species with EFNs (Table 1, Fig. 8). This suggests an independent origin of EFNs within this subfamily that is phylogenetically isolated with respect to the other EFN-bearing lineages (Fig. 2). Known for its taxonomic complexity, *Bauhinia* is currently undergoing a comprehensive systematic revision, with papers on *Phanera* Lour. and *Schnella* Raddi providing necessary combinations in those segregate genera (e.g. Wunderlin 2010; Bandyopadhyay *et al*. 2012; MacKinder and Clark 2014; Trethowan *et al*. 2015). On the basis of the forthcoming new generic classification of this group (C. Sinou, W. Cardinal-McTeague and A. Bruneau, unpubl. data), all species with EFNs in subfamily Cercidoideae belong to *Bauhinia s.str.* The presence of EFNs in *Gigasiphon*, reported to occur on the sepals as an 'apical nectary' (Wunderlin 2010), remains to be confirmed (Table S1).

In *Bauhinia*, all EFNs fall into the embedded subcategory of parenchymatic EFNs and are primarily located around vegetative nodes (i.e. around the insertion of leaves, prickles and other intrastipular structures and stipules on the shoot axes). Only in one species (*B. variegata*, Fig. 8G, H), EFNs occur on the inflorescences, where a nectar droplet accumulates laterally to the bracteoles, but the secretory unit remains unknown. An isolated report of EFNs 'on rachis of compound leaf' in *B. pauletia* (Baker *et al*. 1978, table 1) is unusual and remains to be confirmed.

Intrastipular embedded EFNs have long proven to be useful taxonomically in the American members of *Bauhinia* to differentiate taxa with EFNs from those taxa lacking EFNs, but bearing prickles instead (Bentham 1870). However, this distinction has turned out to be misplaced. Gonzalez and Marazzi (2018), who studied *B. forficata* subsp. *pruinosa*, found that the EFN tissue is completely embedded in the young prickle, which itself is secretory (Fig. 5A, C, 8C, D). In this case, the surface of the prickle is smooth and lacks pores or stomata for nectar release; instead, the cuticle is significantly thinner in the secretory area (Gonzalez and Marazzi 2018). Prickles of *B. forficata* are not modified stipules and represent the first documented case of secretory prickles in legumes. All other intrastipular nectaries described so far in *Bauhinia* appear to be homologous with these secretory prickles, including those that characterise species of the traditionally recognised section *Pauletia* (da Fonseca Vaz and Tozzi 2005). They have been described as 'intrastipular secretory trichomes' (Oliveira and Freitas 2004, fig. 1B), or 'calyciform and elevated' EFNs (Rezende *et al*. 1994; Melo *et al*. 2010*a*, 2010*b*).

The EFNs in subfamily Cercidoideae remain the least well understood in the Leguminosae. Although EFNs appear to be limited to the *Bauhinia s.str.* clade, they may have been overlooked in the genera segregated from *Bauhinia s.l.*, and might, therefore, be more widespread in Cercidoideae than is currently documented. As noted also by Gonzalez and Marazzi (2018), thorough field-based phenological and anatomical investigations are needed to show other cryptic EFNs that are visible only during particular plant ontogenetic or phenological stages. For instance, because they are rather cryptic, the apparently vestigial EFNs reported in some species of *Bauhinia*, such as *B. cheilantha* (Melo *et al*. 2010*b*), might, in fact, secrete nectar at other stages or under different conditions from those observed by these authors. In addition, so as to verify the occurrence of EFNs in unstudied taxa, comparative anatomical studies are necessary to assess organ identity and, hence, the homology of the intrastipular embedded EFNs, as well as to show the structure of the unknown inflorescence EFNs. Furthermore, ant–EFN interactions remain unstudied in *Bauhinia* and, to our knowledge, no ecological studies involving EFNs have been published so far for this genus. Filling all these gaps will be crucial, so as to infer an accurate picture of the occurrence of EFNs in this subfamily and to understand their evolutionary history and significance in relation to other types of EFNs found elsewhere in the family.

Detarioideae

Of the 84 genera in subfamily Detarioideae (like Cercidoideae, this subfamily was also formerly placed in the more broadly circumscribed Caesalpinioideae; Legume Phylogeny Working Group 2017), up to 19 genera apparently include species with EFNs (Table 1, Fig. 9; and eight unclear reports of EFNs need further investigations as to whether the mentioned structures are EFNs; Table S1). This is a significant increase in the number of genera documented to possess EFNs in this subfamily compared with previous studies, and, notably, approximately three times as many as listed by Koptur (1992*a*). Previously Mckey (1989) had concluded that EFNs were confirmed only in one genus, *Leonardoxa*, although he suspected that EFNs were more widespread in this clade. The new data presented here suggest that EFNs are found in genera scattered across the subfamily, except for tribes Schotieae and Barnebydendreae (*sensu* de la Estrella *et al*. 2018); however, even for these tribes, absence needs to be confirmed. EFNs in Detarioideae have been overlooked probably because most species form large trees not easy to study in the field, and field work has focused more on flower morphology and phenology, and not leaf development. Furthermore, in most cases, detarioid EFNs are small, cryptic and not easily visible on herbarium specimens without a hand-lens. Detarioid EFNs are all parenchymatic (Tables 3, 4, Fig. 9), occur exclusively on the lamina of leaflets, and may be flat or embedded (characterising most genera), or occasionally elevated on leaflet margins, which are more conspicuous (Fig. 9J, K). Another reason why EFNs have been overlooked in Detarioideae is perhaps that this clade is well known for another kind of secretory structure, namely, resin-producing glands.

Researchers have long been intrigued by resin-producing detarioid genera. The resin is composed of various sesquiterpenes and diterpenes secreted by epithelial cells that line small pockets, i.e. intercellular spaces produced schizogenously (Langenheim 1981, 2003). These pockets are visible on the surfaces of leaflets (and elsewhere on the plant) as translucent dots (also called 'punctae', Dwyer 1951, or simply punctate glands). Their anatomy and ecological roles in plant defence have been investigated in detail, especially in the genus *Hymenaea* (e.g. Langenheim 1967; Langenheim *et al*. 1982, and references therein). In contrast to this interest in resin-production, EFNs in *Hymenaea* (e.g. Paiva and Machado 2006), and several other detarioid genera (e.g. *Copaifera*, Oliveira and Isaias 2010; *Cynometra*, A. Radosavljevic and I. Coutinho, unpubl. data), have been studied anatomically only recently. Resin-producing detarioids are now known to be restricted to a subclade within tribe Detarieae (Fougère-Danezan *et al*. 2007; de la Estrella *et al*. 2018), suggesting no evident correlation between the presence of EFNs and resin glands, although this needs further study, and their relative ecological roles in plant defence strategies remain poorly understood.

Although most detarioid EFNs are rather cryptic to the untrained eye, Detarioideae, nevertheless, include two well-studied myrmecophyte genera, *Humboldtia* and *Leonardoxa*, belonging to unrelated clades within tribe Amherstieae (de la Estrella *et al*. 2018). These genera possess domatia in addition to their flat and embedded EFNs respectively. Species of the small Indian and Sri Lankan genus *Humboldtia* display a range of specialised myrmecophytic interactions, including true myrmecophytes in which domatia are consistently formed (e.g. *H. laurifolia*; Krombein *et al*. 1999), hemi-myrmecophytes in which only some individuals of a population form domatia (e.g. *H. brunonis*; Gaume *et al*. 2005; Shenoy *et al*. 2012; Chanam *et al*. 2014), and non-myrmecophytes that lack domatia or any resident ant colony and simply attract ants to leaf EFNs (e.g. *H. unijuga*; Krombein *et al*. 1999). Domatia of *Humboldtia* are particularly interesting because of the highly diverse invertebrate fauna they harbour in addition to ants (e.g. Krombein *et al*. 1999; Rickson *et al*. 2003), which include the plant's pollinators (Shenoy and Borges 2008).

The monospecific African genus *Leonardoxa*, comprising four subspecies that make up the *Leonardoxa africana* complex, has been investigated in detail since the early 1980s (e.g. Elias 1980; Mckey 1984). Domatia are consistently present in mature individuals of this species complex, but there is infraspecific variability in the timing of development of the first domatia during plant ontogeny, i.e. the seedling stage, and in the amount of extrafloral nectar produced (Brouat and Mckey 2000). *Leonardoxa* has emerged as a model system for investigating the evolutionary ecology of ant–plant symbioses (e.g. Heil and Mckey 2003, and references therein; Brouat *et al*. 2004; Léotard *et al*. 2008; Blatrix *et al*. 2012). These studies have shown that co-evolutionary interactions with ants can be an important factor driving infraspecific differentiation (Mckey 2000) and have shown novel tripartite co-evolutionary interactions involving the myrmecophytic plant, its associated ants and fungi (e.g. Defossez *et al*. 2009).

Detarioideae is the legume subfamily in which further research on EFNs is most likely to produce exciting new discoveries, not only in terms of their phylogenetic distribution, morphological and anatomical diversity and evolution within the subfamily, but also their ecological and evolutionary roles. In this respect, studies in *Humboldtia* and *Leonardoxa* serve as exemplars to explore ant–plant interactions in the other detarioid genera with EFNs, where such interactions have yet to be investigated in detail.

Caesalpinioideae

Under the new subfamily classification of legumes (Legume Phylogeny Working Group 2017), subfamily Caesalpinioideae was re-circumscribed as a clade that excludes Cercidoideae, Detarioideae, Dialioideae and Duparquetioideae, but which now includes the nested mimosoid clade (former subfamily Mimosoideae; Fig. 2), and now comprises ~150 genera and ~4400 species (Legume Phylogeny Working Group 2017). Within the mimosoid clade, 87 genera are currently recognised, on the basis of the generic list in Legume Phylogeny Working Group (2017) plus three new mimosoid genera, i.e. *Lachesiodendron*, *Parasenegalia* and *Pseudosenegalia*, described since then. It is within this new-sense subfamily Caesalpinioideae, and especially the mimosoid clade, where the greatest concentration, diversity and abundance of EFN-possessing taxa within the legumes occur. Indeed, 87 genera, i.e. well over half of the caesalpinioid genera, possess EFNs, and, within the mimosoid clade, 78 of the 87 genera currently recognised, or 90%, possess EFNs (Tables 1, 2). This represents a major update on previous surveys of caesalpinioid EFNs (Lewis and Elias 1981; Mckey 1989; Pascal *et al*. 2000), plugging many generic gaps and updating generic delimitation (Table 1). Five of the mimosoid genera lacking EFNs (*Amblygonocarpus*, *Aubrevillea*, *Elephanthorriza*, *Fillaeopsis* and *Tetrapleura*) are early branching lineages in the mimosoid phylogeny. Across most of the core mimosoid clade, EFNs are universal except for three apparently independent evolutionary losses of EFNs involving just four genera (see below). In all but a handful of EFN-possessing Caesalpinioideae genera (*Chamaecrista*, *Entada*, *Mimosa*, *Pentaclethra*, *Senna*, *Zapoteca*), occurrence of EFNs within genera appears to be constant, being either present or absent. Taken together, these numbers suggest that more than 3000 of the 4400 species of Caesalpinioideae are likely to possess EFNs. Nowhere else within the legumes are EFNs so prevalent, abundant and conspicuous as within Caesalpinioideae.

It is also within subfamily Caesalpinioideae that three of the legume myrmecophyte lineages, i.e. true ant plants with domatia, are found, including the emblematic swollen-thorn ant 'acacias' in the genus *Vachellia* in Africa and the Neotropics (Janzen 1974; Mckey 1989; Mayer *et al*. 2014, Chomicki *et al*. 2015) and in the genus *Tachigali*, albeit, in this case, the mutualism lacks EFNs (Mckey 1989; Chomicki *et al*. 2015). The Neotropical *Vachellia* myrmecophyte lineage with 12–15 species is often cited as one of the best-studied examples of co-evolution involving an obligate symbiotic mutualism between the *Pseudomyrmex ferrugineus* group of ~10 species of ants that all nest exclusively in the swollen stipular spine domatia of *Vachellia* species (Janzen 1966, 1974; Gómez-Acevedo *et al*. 2010). In return, the nectar from the multiple conspicuous EFNs on the petiole and leaf rachis (see Fig. 13O), as well as specialised beltian food bodies on the tips of the leaflets, are specific for the resident ants (Heil 2004; Heil *et al*. 2009). Studies of these spectacular protective ant–acacia mutualisms, alongside those on *Chamaecrista* (especially *C. fasciculata*; Barton 1986; Kelly

1986; Rutter and Rausher 2004) and *Inga* (e.g. Koptur 1984, 1985, 1994), were among the first in-depth studies of the protective function of EFNs in obligate and facultative ant–plant mutualisms respectively, and have made important contributions to understanding of the ecology of myrmecophytes more generally (e.g. Heil and Mckey 2003). It is also notable that another legume, the Australian *Acacia terminalis*, is the only example, to our knowledge, of EFNs as an adaptation to bird pollination (Knox *et al*. 1985).

Many of the non-mimosoid Caesalpinioideae genera and almost all mimosoid genera have bipinnate leaves (with the notable exceptions in the mimosoid clade of the genus *Inga* and *Cojoba rufescens*, which have once-pinnate leaves), and EFNs in Caesalpinioideae are largely restricted to genera with bipinnate leaves, with only a few exceptions, notably *Senna*, *Chamaecrista* and *Inga*. In the large majority of caesalpinioid genera, EFNs are conspicuous raised structures classified as elevated parenchymatic leaf nectaries that are visible on dried herbarium specimens. Although most species possess a single petiolar EFN per leaf, in many species, multiple EFNs are present on the petiole, along the primary leaf rachis at the point of insertion of some or all of the leaflets or pinnae (also called jugal EFNs) and very frequently between the terminal pair of leaflets and pinnae. For some genera with bipinnate leaves, EFNs are also found along the secondary rachises at the point of insertion of the terminal pair(s) of leaflets. In a few species, EFNs have proliferated, with up to 75 EFNs being observed on a single leaf (e.g. *Leucaena trichandra*, Hughes 1998). It is clear that the compound leaf, and especially the evolutionarily labile and highly variable bipinnate leaf formula prevalent across Caesalpinioideae, provides a flexible and powerful template for legumes to fine-tune exactly where and when during development EFNs are activated and presented to ants in return for protection.

These elevated Caesalpinioid EFNs are extremely diverse in shape and size, and include sessile or stalked nectaries, rounded, oval, elliptic, crateriform, patelliform, verruciform, slit-like and cupular (Fig. 10–13). This morphological diversity is attributable to the protruding morphologies that allow elevated EFNs to occupy morphological space independent of that of their bearing organs, an idea embodied by the concept of EFN individualisation (Marazzi *et al*. 2013*b*). Increasing individualisation (i.e. the more an EFN protrudes from the surface) is associated with increasing disparification of EFNs, which are decoupled from the constraints of their bearing organs, culminating in the more elaborate stalked or sessile convex morphologies of elevated EFNs (see examples in Fig. 10, 11; see in the following paragraphs).

This diversity in form and size of elevated EFNs is apparently evolutionarily highly labile, with repeated occurrences of similar suites of morphologically diverse EFNs within many mimosoid genera (e.g. *Archidendron*, Nielsen *et al*. 1984; *Leucaena*, Hughes 1998; *Desmanthus*, Luckow 1993; *Inga*, Pennington 1997; *Senna*, Marazzi *et al*. 2013*b*). In a few cases, more conspicuous larger or unusually shaped nectaries have been observed, such as the following: double heart-shaped nectaries in *Parkia*, sometimes two or three EFNs at each point of insertion of leaflet pairs on the once-pinnate leaves of *Inga* species; enlarged conspicuous coloured funnel-shaped nectaries up to 12 mm in length (*Abarema adenophora*) or campanulate and becoming subligneous up to 11 mm in length (*Abarema macradenia*); nest-shaped nectaries with the orifice pointing upward or the upper part bent over the cavity as a lid (*Archidendron merrillii* and *A. crateradenum* respectively, Nielsen *et al*. 1984, fig. 18); stalked nectaries with a clavate head (*Inga allenii*); enlarged cup-shaped nectaries up to 7.4 mm in diameter (*Pithecellobium macradenium*; references in Table 1); in *Acacia terminalis* red-coloured EFNs attract birds that consume nectar and can act as pollinators (Knox *et al*. 1985).

In many cases, fully developed, enlarged and functional EFNs are present even on the reduced leaves subtending inflorescences that sometimes show partial and incomplete development, in line with the idea that EFNs are most active on young developing leaves (Mckey 1989). In extreme cases, highly reduced leaves are produced that appear to be completely truncated after formation of a fully functional EFN, especially for species that have extensive compound panicles of capitula, such as *Leucaena esculenta* (Fig. 13E, F) and *Parasenegalia santosii* (fig. 42 in Rico-Arce 2007), such that just the petiole and EFN are present.

Aside from this general pattern of occurrence of leaf nectaries, EFNs in Caesalpinioideae have also been reported in a few scattered taxa from other plant organs, including (1) in the genus *Senna* on inflorescence axes at the base of bracts, and also with non-elevated EFNs on stipules, bracts and sepals (Marazzi *et al*. 2013*a*; Table 1, Fig. 10F–N), (2) modified stipules (*Archidendron*, e.g. *A. brachycarpum*, *A. molle*; Nielsen *et al*. 1984, fig. 56; Nielsen 1992, fig. 16) or at the base of the stipules or stipule scars (*Piptadeniastrum*), (3) at the base of the floral bracts (*Archidendron* series *Stipulatae* in Asia; Nielsen *et al*. 1984, fig. 59, 65; Nielsen 1992, fig. 17), and *Macrosamanea* in the Neotropics; Fig. 12I, J), (4) on the bracts subtending inflorescences (*Calpocalyx*) and (5) on the stems (*Entada phaseoloides*, *Pentaclethra macroloba* (Fig. 13D, E) and *Pseudoprosopis sericeus*).

Thus, in both the genus *Senna* and across much of the mimosoid clade and within many mimosoid genera, EFNs show their greatest proliferation and morphological disparification, this involving multiple locations on the same plant (e.g. on leaves and inflorescence bracts), multiple locations on the same EFN-bearing organ (e.g. petiole and between leaflets and pinnae), and highly individualised morphologies (e.g. shapes, colours and sessile *v.* stalked).

Ancestral reconstruction of EFNs across Caesalpinioideae (Fig. 2) suggests a complex pattern of multiple independent gains (and potentially some losses) across non-mimosoid Caesalpinioideae and the first-branching lineages within the mimosoid clade. However, within core mimosoids, EFNs are almost universal apart from three clear cases of the evolutionary loss of EFNs. First, EFNs are absent for species of the genera *Acaciella*, *Calliandra*, and its recently segregated sister genus *Afrocalliandra* (the latter despite suggestions in the original description of this genus (de Souza *et al*. 2013) that one of the two species possesses EFNs, it is now clear that this is not the case; see Tables 1, S2). In forthcoming mimosoid phylogenies, these three genera form a clade (E. J. Koenen, unpubl. data), suggesting a single loss in this part of the phylogeny. A second loss is postulated within the genus *Mimosa* where EFNs have been reported to be restricted to section *Mimadenia*, which is

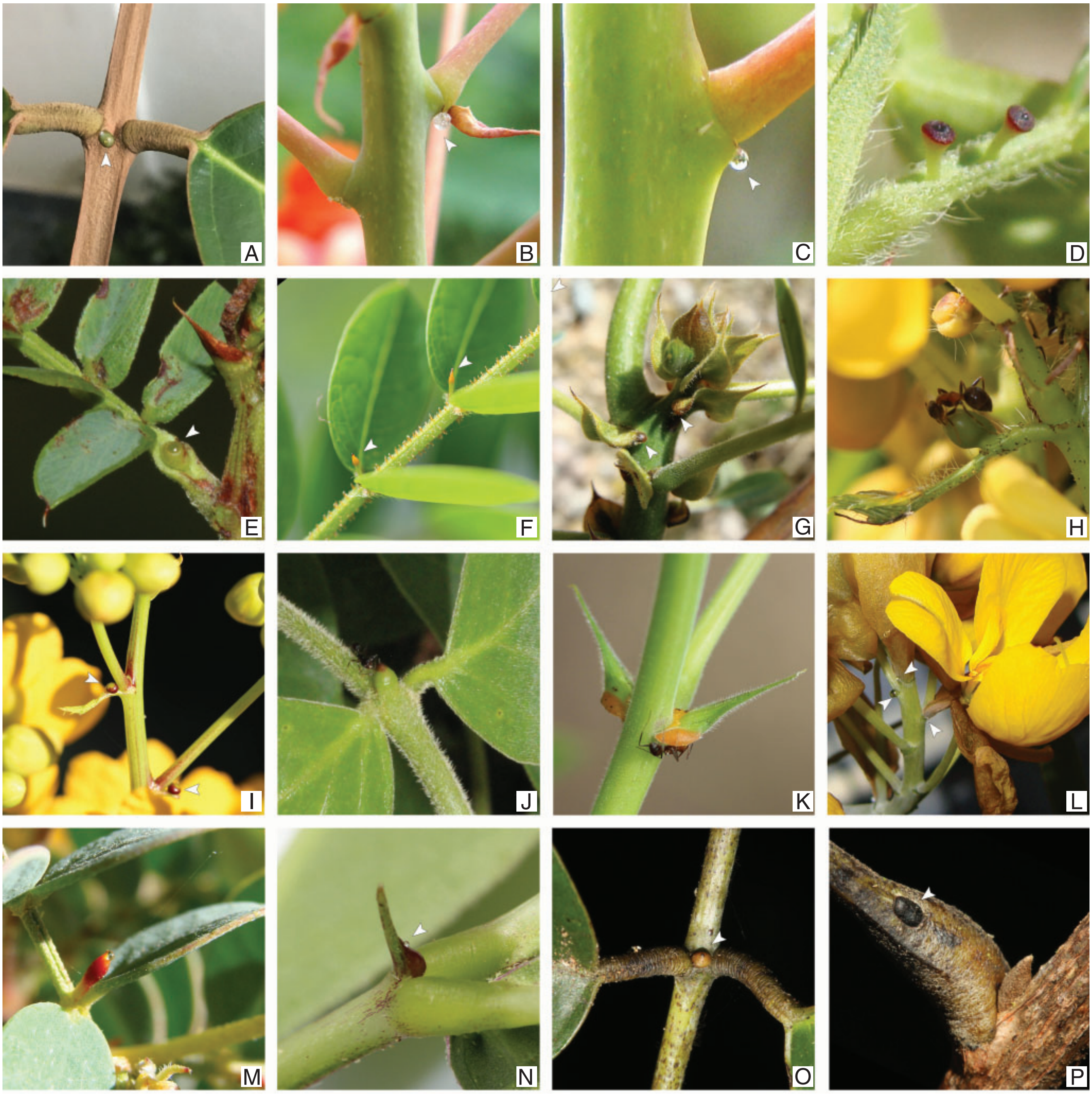

Fig. 10. Diversity of extrafloral nectaries (EFNs) in Caesalpinioideae. Arrowheads indicate positions of EFNs. EFN categories are as follows: non-differentiated abscission zone EFNs (B, C, L); all others are parenchymatic elevated, except those that are flat (G, K). A. *Batesia floribunda*, rachis. B, C. *Caesalpinia pulcherrima*, inflorescence axes. D, E. *Chamaecrista nictitans*, petiole. F. *Senna acuruensis*, rachis. F. *Senna didymobotrya*, stipule lobes. H. *Senna hebecarpa*, bract petiole. I. *Senna mexicana*, bract petiole. J. *Senna* cf. *macranthera*, rachis. K. *Senna martiana*, lobe of stipules. L. *Senna pleurocarpa*, inflorescence axis. M. *Senna purpusii*, rachis. N. *Senna scabriuscula*, mucro. O, P. *Vouacapoua americana*, rachis and petiole. Photos: Matheus Cotta (A) and Domingos Cardoso (O, P).

sister to the rest of the genus (Barneby 1991; Simon *et al*. 2011). However, more recently, Gonzalez and Marazzi (2018) showed that *Mimosa bifurca*, which is placed in series *Stipellares* of section *Batocaulon* and is nested deep within *Mimosa* (Clade K in Simon *et al*. 2011) possesses EFNs, suggesting that with more careful observations, additional species of *Mimosa* with EFNs may well be discovered in the future. It is perhaps notable that the EFN-possessing Mimadenia clade of *Mimosa* comprises mainly lianas in Amazonian rainforest, in line with the idea that EFNs are especially common on leaves of lianas, which have a continuous production of young leaves (Mckey 1989). Finally, in the genus *Zapoteca*, only 3 of the ~20 species possess EFNs (Hernández 1989). Given that *Zapoteca* is deeply nested within the large EFN clade of mimosoids and that the three EFN-possessing species

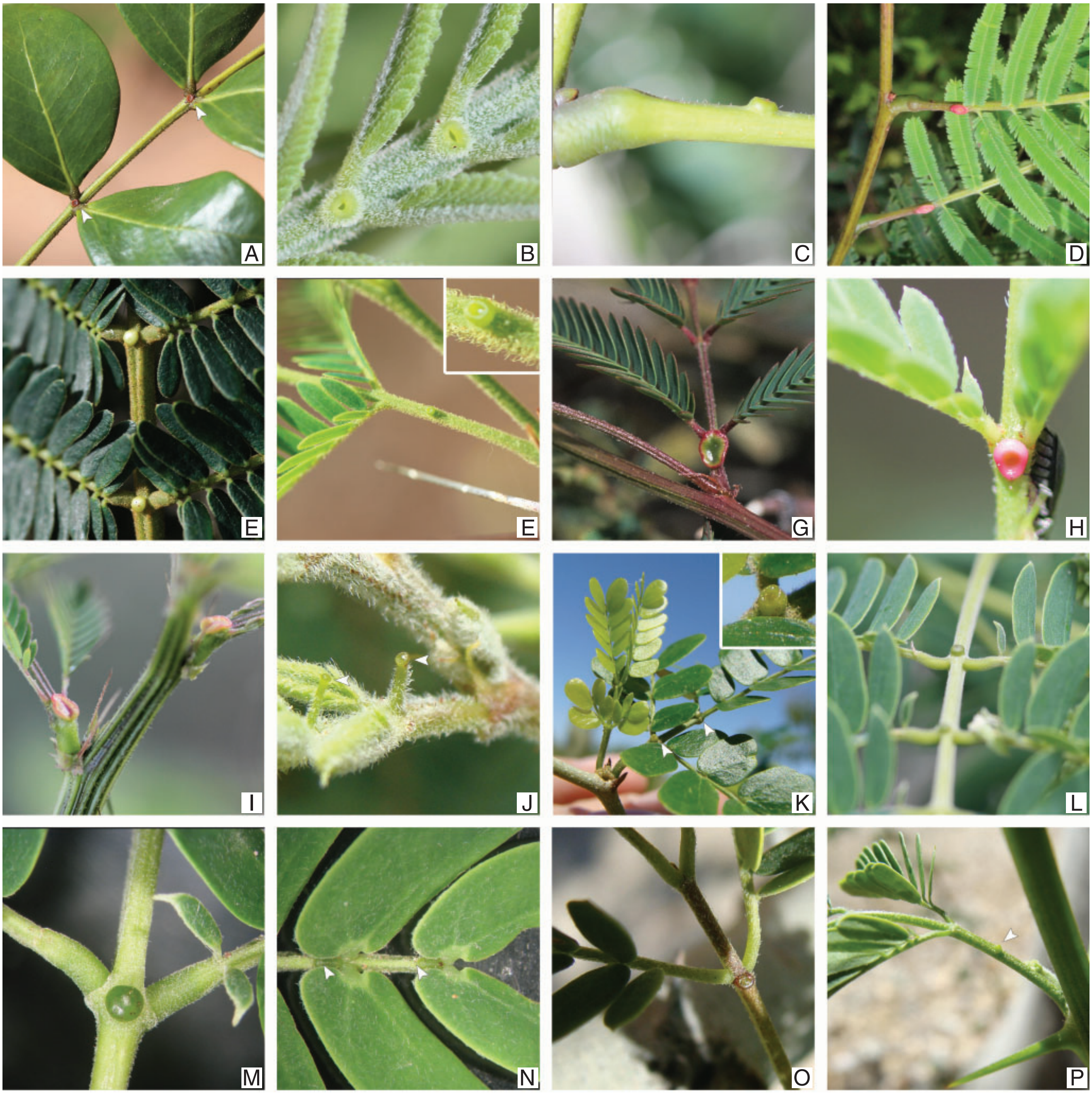

Fig. 11. Diversity of extrafloral nectaries (EFNs) in the Mimosoid clade (Caesalpinioideae), Part 1 (genera A–H). Arrowheads indicate positions of EFNs. All EFNs are parenchymatic and elevated. A. *Abarema cochliacarpos*, rachis. B. *Acacia dealbata*, rachis. C. *Albizia julibrissin*, petiole. D. *Anadenanthera colubrina*, petiole. E. *Balizia pedicellaris*, rachis. F. *Chloroleucon acacioides*, petiole; close up of EFN in box. G. *Desmanthus acuminatus*, petiole. H. *Desmanthus covillei*, rachis. I. *Desmnathus pernambucanus*, rachis (photo: Luciano P. de Queiroz). J. *Dichrostachys cinerea*, rachis. K. *Ebenopsis flexicaule*, rachis; close up of EFN in box. L. *Enterolobium timbouva*, rachis. M, N. *Enterolobium contortisiliquum*, leaf and pinnular rachises. O, P. *Havardia pallens*, rachis and petiole.

comprise the first branching lineages within the genus (Ferm 2019), this implies one other loss of EFNs within the mimosoid clade. In a few species in other genera (e.g. *Albizia*), EFNs have apparently become highly reduced or even obsolete.

The idea that there could be an association or correlation between the presence of EFNs and nodulation was suggested by Mckey (1989), perhaps reflecting underlying ecological differences related to competitive strategies and the phenology of leaf production. Our survey provides some tantalising hints supporting this idea within Caesalpinioideae, in that all the genera of early branching mimosoids that lack typical elevated caesalpinioid EFNs (*Adenanthera*, *Amblygonocarpus*, *Aubrevillea*, *Fillaeopsis* and *Tetrapleura*) are either known to be non-nodulating or of unknown

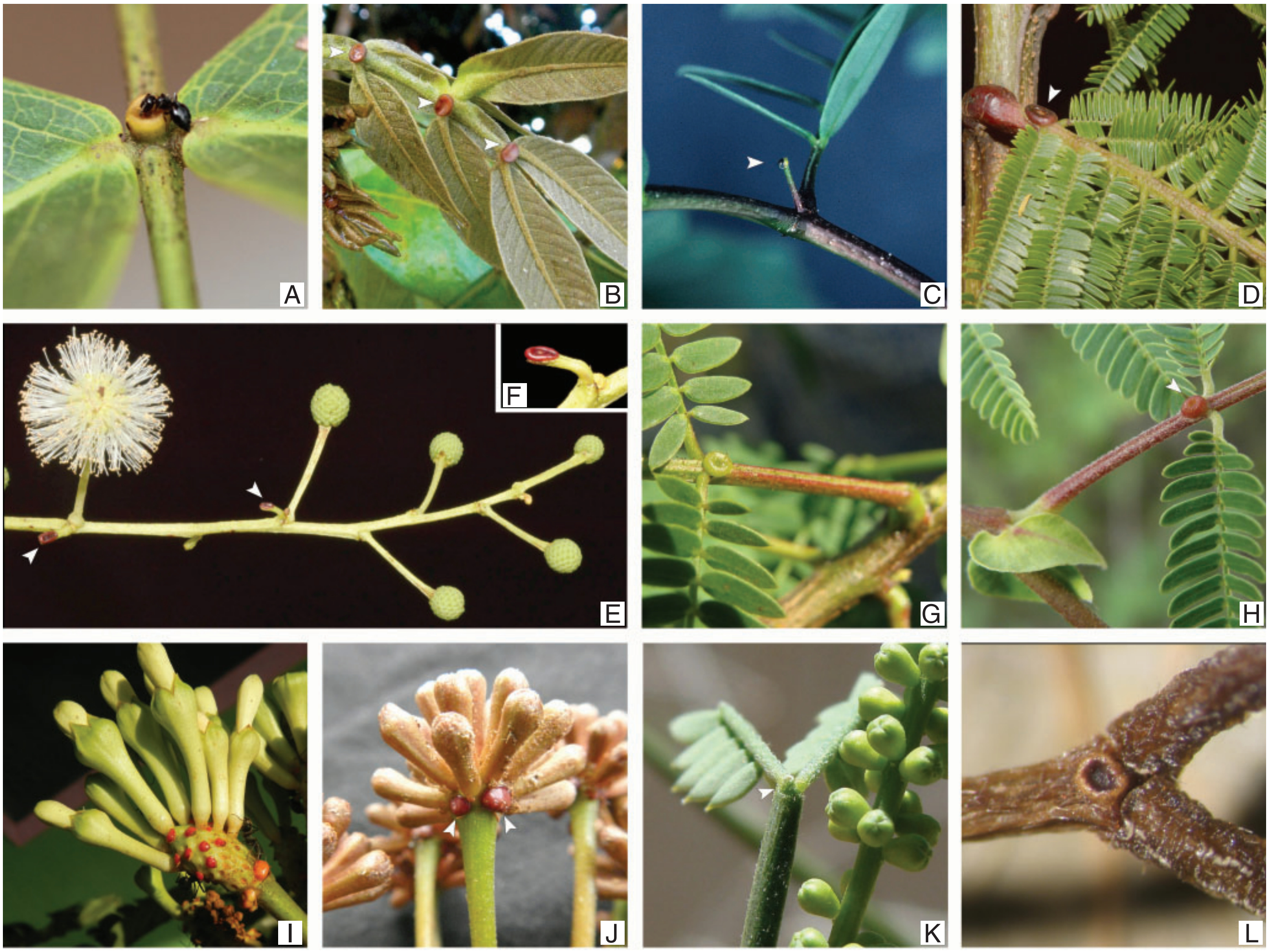

Fig. 12. Diversity of extrafloral nectaries (EFNs) in the Mimosoid clade (Caesalpinioideae), Part 2 (genera I–M). Arrowheads indicate positions of EFNs. All EFNs are parenchymatic and elevated. A. *Inga cayensis*, rachis. B. *Inga edulis*, rachis. C. *Leucaena greggii*, rachis. D–F. *Leucaena esculenta*, petiole, inset showing reduced leaves (bracts) where leaf development is truncated after formation of just the petiole including a fully functional petiole EFN (see text). G. *Leucaena leucocephala*, petiole. H. *Lysiloma divaricatum*, petiole. I. *Macrosamanea amplissima*, at base of caducous floral bracts on inflorescence axis. J. *Macrosamanea pubiramea*, inflorescence axis. K. *Mariosousa willardiana*, rachis. L. *Microlobius foetidus* subsp. *paraguariensis*, rachis (herbarium specimen). Photos: Oscar Dorado and Karime López (D–F) and Erik Koenen (B, I, J).

nodulation status (Sprent 2009). Similarly, it is striking that in the genus *Pentaclethra*, the African species *P. macrophylla* is non-nodulating and lacks EFNs, whereas the American species *P. macroloba* is nodulating and possesses EFNs on the stems. However, beyond these striking examples, there are many nodulating taxa that lack EFNs (e.g. *Calliandra*, *Acaciella*, *Campsiandra*, *Melanoxylon* and *Moldenhawera* and, of course, the majority of Papilionoideae), suggesting that this association, if it is significant, is a rather loose one.

Papilionoideae

Of the six subfamilies, Papilionoideae is the largest, comprising over 500 genera, but it includes only 46 genera with EFNs (Tables 1, 2). Therefore, in Papilionoideae absence of EFNs is clearly prevalent, especially compared with subfamilies Caesalpinioideae and Detarioideae where presence of EFNs predominates (Fig. 2, Table 2). This proportionately low number of Papilionoideae genera with EFNs is even more stark, considering that our account lists almost three times more papilionoid genera with EFNs than did previous summaries by Mckey (1989) and Koptur (1992*a*). Although this increase is, in part, because of generic splitting, it does not take into account that some of the genera previously listed are not confirmed here (Table S1). Despite the relatively sparse occurrence of EFNs in Papilionoideae, their phylogenetic distribution indicates several independent evolutionary origins scattered disparately across the subfamily (Fig. 2A), involving various types of EFNs, and with the majority being concentrated in tribe Phaseoleae.

Four EFN genera of the early diverging lineages of the ADA clade (consisting of the Angylocalyx, Dipterygeae and Amburana clades; Cardoso *et al.* 2012, 2013), *Alexa* and *Castanospermum* (both tribe Angylocalyceae), *Monopteryx*

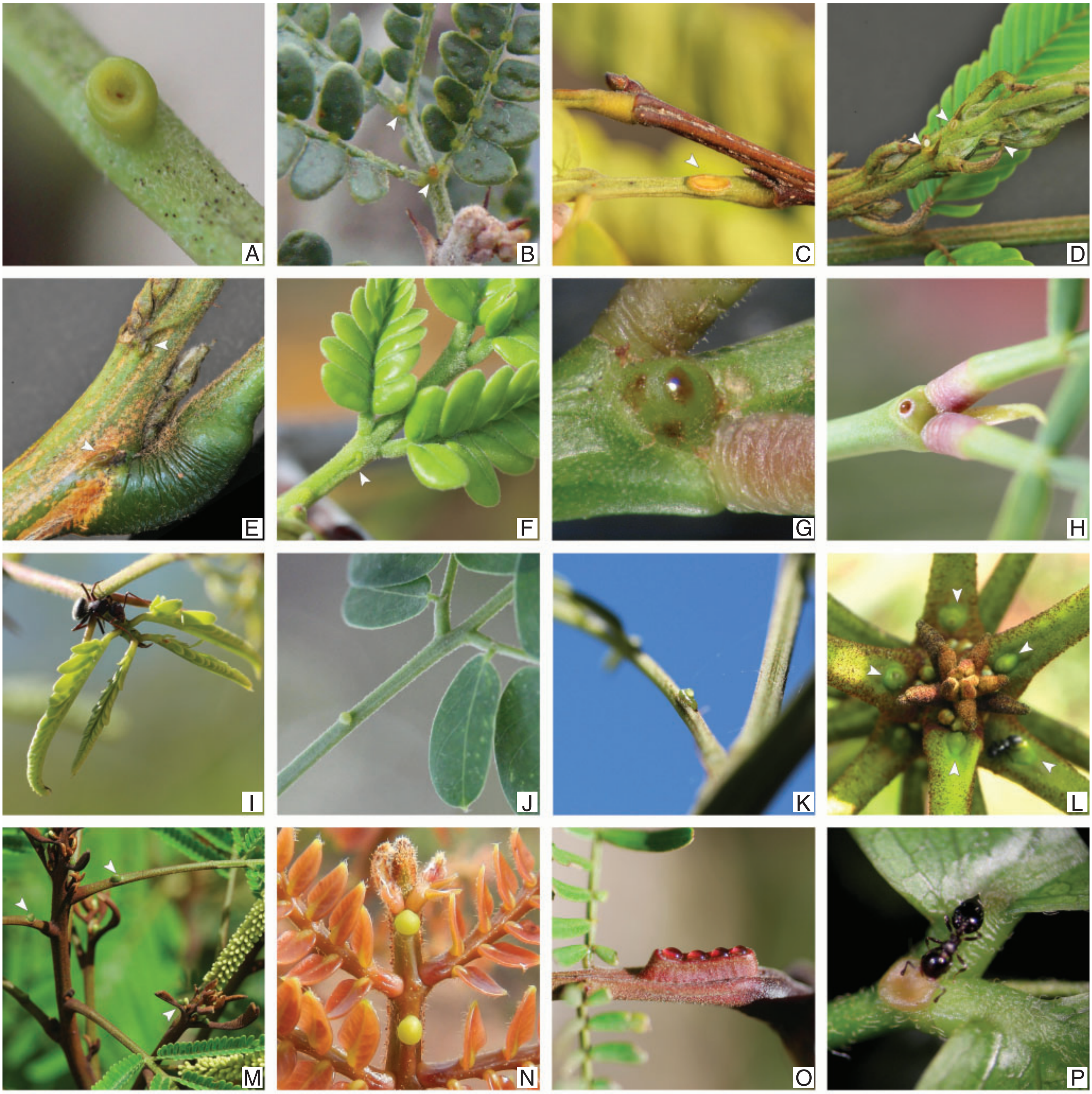

Fig. 13. Diversity of extrafloral nectaries (EFNs) in the Mimosoid clade (Caesalpinioideae), Part 3 (genera M–Z). Arrowheads indicate positions of EFNs. All EFNs are parenchymatic and elevated. A. *Mimosa irrigua*, petiole. B. *Painteria elachistophylla*, rachis. C. *Parapiptadenia* sp. indet., petiole. D, E. *Pentaclethra macroloba*, stem below stipule in leaf axil. F. *Pityrocarpa moniliformis*, petiole. G. *Prosopis alba*, rachis. H. *Prosopis nigra*, rachis. I. *Prosopis* sp. indet., rachis. J. *Pseudopiptadenia* sp. indet., petiole. K. *Senegalia bonariensis*, petiole. L. *Stryphnodendron adstringens*, petiole. M. *Stryphnodendron pulcherrimum*, petiole. N. *Stryphnodendron rotundifolium*, rachis of young developing leaf. O. *Vachellia collinsii*, petiole. P. *Zygia morongii*, rachis. Photos: João Paulo Basso-Alves (D, E), Thais Cury de Barros (L), Martin Heil (O) and Erik Koenen (N).

and *Pterodon* (both Dipterygeae), are clearly isolated within the subfamily. The rest of the papilionoid EFN genera occur in the large 50-kb inversion clade (cf. Fig. 2 in the present study with fig. 1 in Cardoso *et al*. 2013). The occurrence of EFN genera in these early branching papilionoid lineages contrasts with earlier hypotheses of EFN evolution in Papilionoideae, which suggested that papilionoid EFNs had evolved in more derived groups and were absent from early branching papilionoid lineages (Lersten and Brubaker 1987; Mckey 1989). Moreover, these isolated reports of ADA clade EFNs are the only ones of parenchymatic EFNs in Papilionoideae, being flat in *Alexa* and its sister genus *Castanospermum* and elevated in

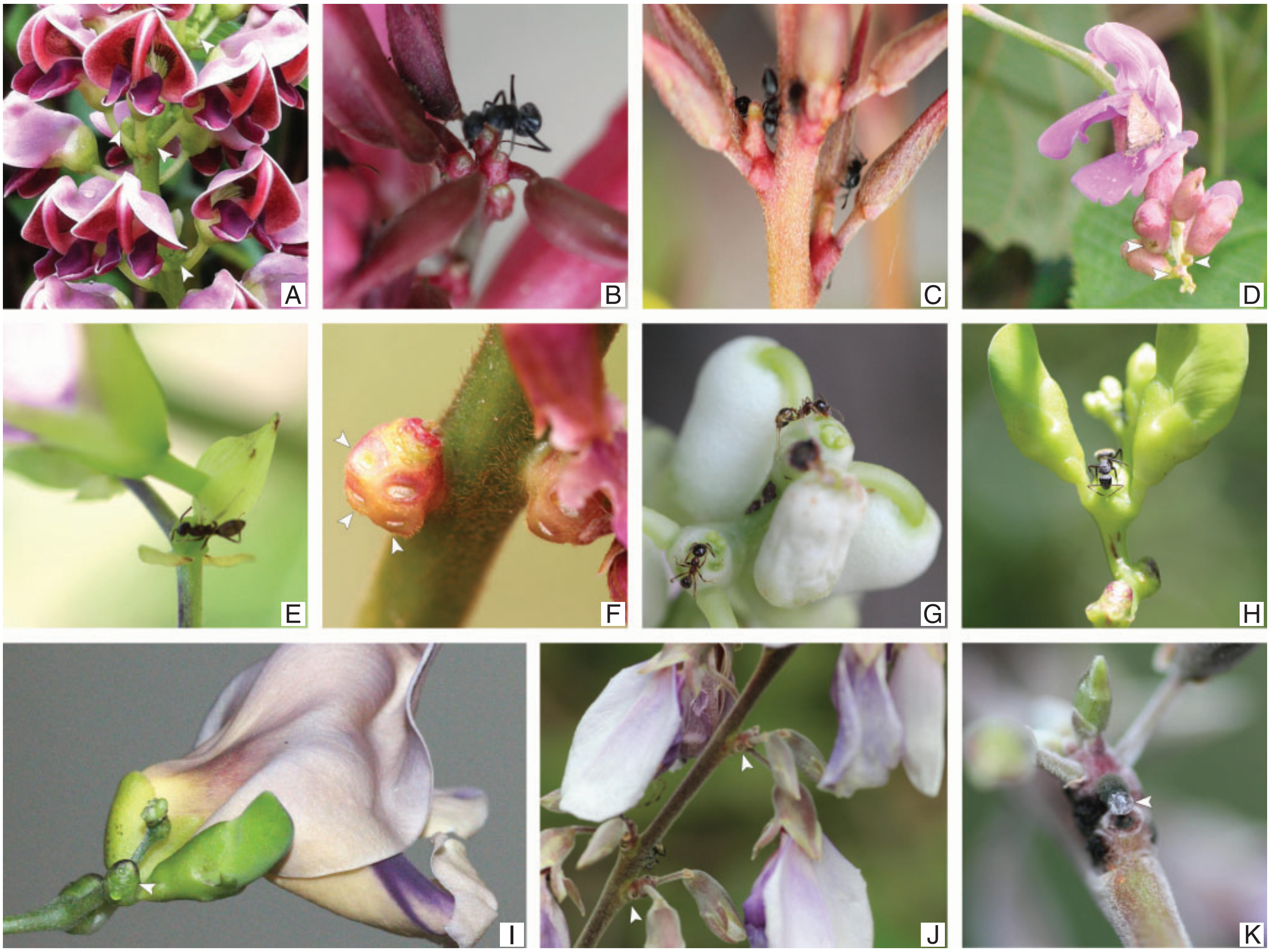

Fig. 14. Diversity of extrafloral nectaries (EFNs) in Papilionoideae, Part 1 (genera A–C). Arrowheads indicate positions of EFNs. All swollen-scar (abscission-zone) EFNs, from aborted buds. A. *Apios americana* (photo: Nicola Patocchi). B, C. *Bionia coriacea.* D. *Canavalia bonariensis.* E. *Centrosema virginianum.* F. *Cleobulia multiflora.* G. *Cochliasanthus caracalla.* H, I. *Condylostylis* cf. *candida.* J, K. *Cratylia mollis.*

Monopteryx and *Pterodon*. The latter are strongly reminiscent of caesalpinioid elevated EFNs (see references in Table 1, Fig. 15C), and are apparently homoplasious across these different groups, but the primary homology of these distantly related elevated parenchymatic EFNs remains speculative, because the ADA clade EFNs remain poorly studied and understood. It is also possible that EFNs have been overlooked or confused with other secretory structures in the ADA clade. For instance, *Pterodon* also possesses oil glands (Rodrigues *et al*. 2011), although anatomical analyses suggest that these are distinct from the elevated EFNs in this genus. Thorough investigation of the occurrence of EFNs in these early papilionoid lineages is needed to obtain a more complete picture of the evolution of elevated EFNs in Leguminosae and to address the question of why the Papilionoideae did not develop elevated EFNs in more taxa.

Another phylogenetically isolated occurrence of EFNs within Papilionoideae are the scattered occurrences of EFNs within the genus *Crotalaria* (tribe Crotalarieae, genistoid clade; *sensu* Cardoso *et al*. 2013). EFNs have been reliably reported from just 4 of the ~700 species of *Crotalaria*, namely, *C. incana* (e.g. Baker *et al*. 1978), *C. intermedia* (mentioned in Mckey 1989, p. 693), *C. micans* (Noack 1903) and *C. pallida* (Guimarães *et al*. 2006; Pereira and Trigo 2013), but Noack's findings remain unconfirmed (simply cited by Mckey 1989 and Vogel 1998). A fifth EFN-possessing taxon, *C.* aff. *striata* (Noack 1903), is probably best treated as *C. pallida* (G. Lewis, Royal Botanic Gardens Kew, pers. comm.). In *Crotalaria*, EFNs occur on both reproductive and vegetative parts in the form of abscission-zone EFNs on the scars of fallen stipules, prophylls, bracts and flower pedicels (Noack 1903; Mckey 1989; Díaz-Castelazo *et al*. 2005). Detailed anatomical studies are needed to ascertain whether these abscission-zone EFNs are non-differentiated or swollen scars. Recent ecological studies of *C. pallida* (Pereira and Trigo 2013) have shown that these EFNs form part of a complex multispecies interaction involving ants, a specialised seed predator, and predatory wasps.

Among the other 41 papilionoid genera with EFNs (all within the non-protein–amino-acid-accumulating clade, NPAAA; Cardoso *et al*. 2013), *Robinia* represents another poorly known and apparently isolated occurrence of EFNs in the robinioid clade. The morphology and anatomy of the EFNs reported on the stipules and stipels of a single species, *R. pseudoacacia* (Pemberton 1990), are still unknown (see Table 1).

The large majority of papilionoid EFN genera is concentrated within tribe Phaseoleae, except for *Vicia* (Fabeae; see Table 1), and involves two categories of EFNs, namely, trichomatic (exposed or sunken) and abscission-zone EFNs, and notably swollen-scar EFNs (Table 2). Most taxa apparently have either trichomatic EFNs or swollen-scar EFNs, but in three genera, *Dolichos*, *Lablab* and *Vigna*, species bearing both these EFN categories occur simultaneously (Fig. 4D–G, 7H, I, 15M–P respectively). It is possible that more taxa for which only swollen-scar EFNs are currently reported, also bear trichomatic EFNs on the stipules, stipels or both, but this remains to be verified. By contrast, on taxa that have only trichomatic EFNs, the EFNs may be found also in the inflorescences, such as in *Erythrina* on the calyx lobes (Fig. 4K, L) and in *Vicia* on the bracts (Fig. 15L). *Erythrina* is outstanding among Phaseoleae not only for its calyx-lobe EFNs, but also as the only genus of legumes with pericarpial nectaries, i.e. EFNs on the surface of developing fruits (in *E. speciosa*), which are visited by ants (Paiva 2009).

These trichomatic inflorescence EFNs are functionally equivalent to swollen-scar EFNs, in that both attract mutualistic ants to the reproductive parts of the plant (Sherbrooke and Scheerens 1979; Priest and Loveless 2009). In contrast, *Phaseolus* bears trichomatic EFNs on stipels, but lacks inflorescence EFNs (Delgado-Salinas *et al*. 2011). One species of *Phaseolus*, *P. lunatus* L. (Fig. 4H, 15I) has emerged as a model system for investigating the ecological and evolutionary roles of volatile organic compounds in the context of plant defence strategies (e.g. Heil 2004; Choh *et al*. 2006; Godschalx *et al*. 2015). The ecology of EFNs in *Vicia* has also been thoroughly studied (e.g. Koptur 1979; Koptur and Lawton 1988; Mondor and Addicott 2003; Mondor *et al*. 2006; Gish *et al*. 2015).

Swollen-scar EFNs are a distinctive feature of papilionoid legumes (Table 1; Delgado-Salinas *et al*. 2011; Marazzi *et al*. 2012; Gonzalez and Marazzi 2018), displaying diversity in numbers and positions on the inflorescences, depending on the proportions and total numbers of flowers either developing or aborting. For example, these EFNs can be aligned between anthetic flowers (e.g. *Macroptilium prostratum*, Fig. 7E; *Vigna unguiculata*, Fig. 7H) or arranged in a more or less helicoidal order (e.g. *Ancistrotropis peduncularis*, Fig. 7A; *Condylostylis candida*, Fig. 7B; *Macroptilium gibbosifolium*, Fig. 7G). The inflorescence axes themselves can appear short and inflated, bearing multiple swollen-scar EFNs (e.g. *Cleobulia multiflora*, Fig. 15F; *Cochliasanthus caracalla*, Fig. 15 G) and these lateral inflorescences with highly compressed axes (Ojeda *et al*. 2014) are commonly referred to as pseudoraceme nodes (e.g. Delgado-Salinas *et al*. 2011). Swollen-scar EFNs are surely more widespread across Phaseoleae than is currently documented, and detailed mapping of their diversity in terms of numbers, arrangements and the complexity of their inflorescence axes is likely to show interesting evolutionary patterns for this specialised kind of EFN, which is unique within, and most likely beyond, the legume family. The ecological role of swollen-scar EFNs has long remained hypothetical, following the general reasoning that EFNs are usually located on leaves, flowers and fruits, where they develop and start secreting nectar to attract ants at a time when attacks by herbivores, florivores and seed predators would result in the greatest damage (Mckey 1989; Rico-Gray and Oliveira 2007). To our knowledge, this hypothesis has been investigated in only one species, i.e. *Vigna luteola*, by Aguirre *et al*. (2018), who suggested that ants attracted by the swollen-scar EFNs could have a dual function for the plants, namely, protecting them against potential herbivores as well as protecting flowers against nectar thieves. In this case, the presence of ants did not appear to interfere significantly with pollination, because the main pollinator was not deterred by ants.

Several hypotheses and explanations for the absence of EFNs in most of the Papilionoideae have been suggested. Polhill (1994, p. 35) pointed out that, in papilionoids, 'the function of ant attraction [via EFNs] sometimes was replaced by glandular hairs and pearl bodies'. Indeed, other structures, notably glandular trichomes (unicellular and multicellular), for instance, in tribes Indigofereae and Dalbergieae (Polhill 1994; tribes *sensu* Cardoso *et al*. 2013), and some types of hydathodes, pearl bodies, and colleters, have often been misinterpreted as EFNs, probably because of the persistent lack of knowledge concerning their occurrence, contents and functions. The genus *Indigofera* is a good example; ants collect trichome heads found to secrete lipophilic substances (Marquiafável *et al*. 2009) and some hydathodes in this genus have been called 'hydathode extrafloral nectaries' because of their morphological similarity with nectaries (Schrire 1995; Schrire *et al*. 2009).

Another hypothesis could be that Papilionoideae are perhaps more versatile in defending themselves from herbivores than are Caesalpinioideae (including mimosoid legumes), Cercidoideae and Detarioideae by increased toxicity of highly diverse nitrogen-based compounds and other toxic compounds found in this subfamily (Harborne 1994; Zarucchi 1994). Chemical constituents have been named and described, including toxic non-protein aminoacids and peptides, aliphatic nitro-compounds, alkaloids and flavonoid constituents such as flavonol glycosides, isoflavonoids, furano coumarins, and xanthones for the Papilionoideae (see also Wink 2013).

Legume EFNs: a phylogenetic and evolutionary perspective

Accurately documenting and understanding the diversity, phylogenetic distribution and temporal and geographical evolutionary trajectories of EFNs, in terms of evolutionary gains and losses across legumes, is fundamental if we are going to be able to properly assess the significance, origins, maintenance and breakdown of these important evolutionary morphological and functional traits and their mutualisms (e.g. Heil *et al*. 2009; Chomicki and Renner 2015; Chomicki *et al*. 2015). For example, it has been suggested that EFNs could represent a possible key evolutionary innovation, contributing to diversification in the genus *Senna* (Marazzi and Sanderson 2010; but see also Marazzi *et al*. 2013*b*), whereas in another evolutionarily successful genus, *Mimosa*, an apparent evolutionary loss of EFNs coincides with a clade comprising

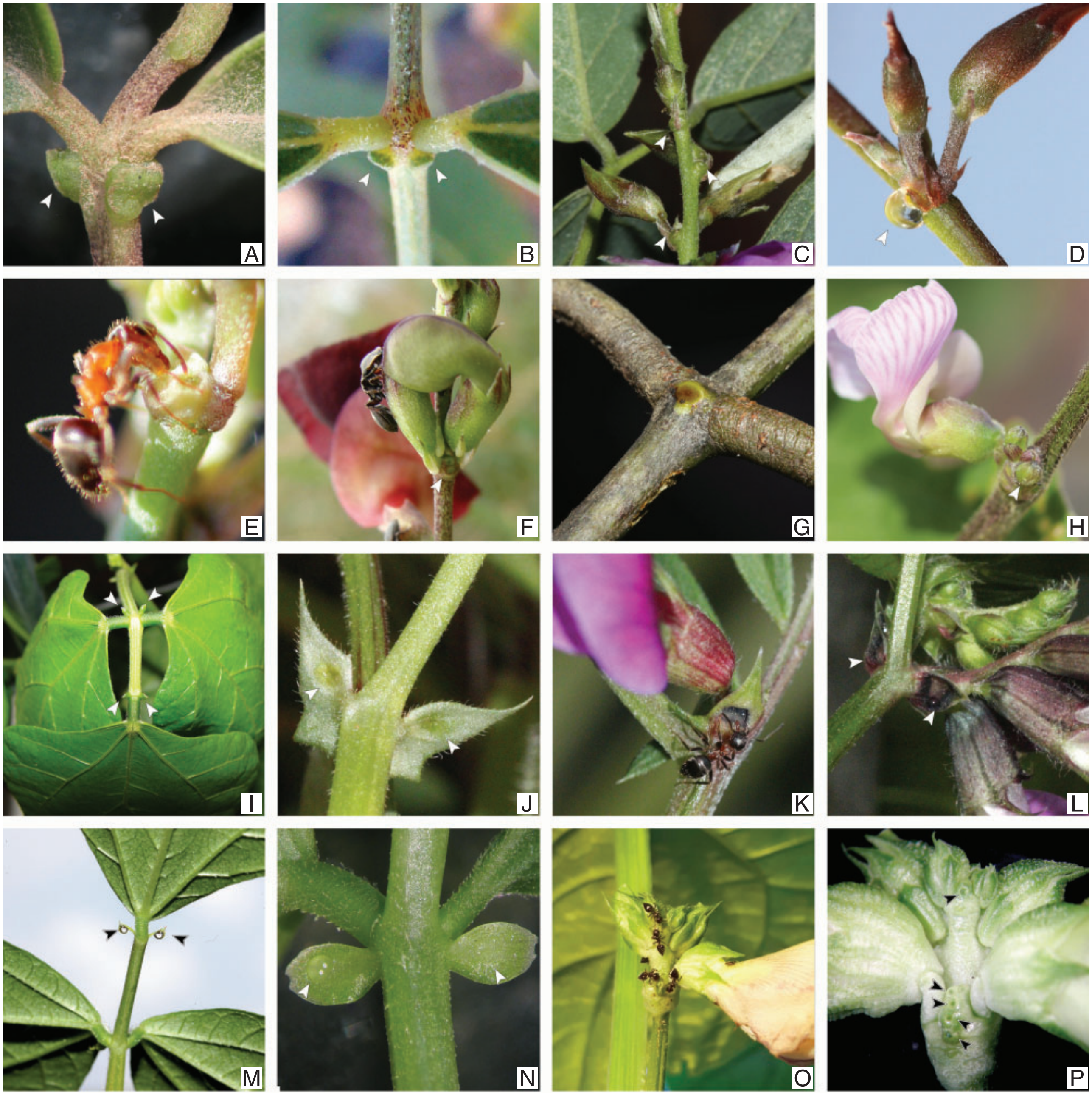

Fig. 15. Diversity of extrafloral nectaries (EFNs) in Papilionoideae, Part 2 (genera E–V). Arrowheads indicate positions of EFNs. Categories of EFNs are as follows: abscission zone and swollen scar (C–F, M, O, P), parenchymatic and elevated (G), trichomatic exposed (J–L, N) and hollow (A, B, I). A. *Erythrina dominguezii*, stipels. B. *Erythrina vespertilio*, stipels. C. *Galactia latisiliqua*, inflorescence axis. D, E. *Kennedia rubicunda*, inflorescence axis. F. *Macroptilium prostratum*, inflorescence axis. G. *Monopteryx uaucu*, leaf rachis. H. *Mysanthus uleanus*, inflorescence axis. I. *Phaseolus lunatus*, stipels. J, K. *Vicia sativa*, stipules. L. *Vicia sepium*, bracts. M. *Vigna radiata*, stipels. N–P. *Vigna unguiculata*. N. stipels. O, P. Inflorescence axis. Photos: Domingos Cardoso (G) and Leticia Torres-Colín (M).

the large majority of the ~550 species in the genus (Simon *et al.* 2011). Losses of mutualisms are also of considerable evolutionary interest (e.g. Gutiérrez-Valencia *et al.* 2017). For example, the multiple losses of EFNs hypothesised in three independent mimosoid clades documented here remain poorly understood, with no obvious environmental or other correlates for the large cohort of EFN-lacking *Calliandra*, *Acaciella*, *Mimosa* and *Zapoteca* species, which span a wide range of neotropical biomes.

In this paper, we map and illustrate the global occurrence of legume EFNs (of all types) on a time-calibrated legume phylogeny (Fig. 2), building on the only previous phylogenetic reconstruction by Marazzi *et al*. (2012), but here using a phylogeny that includes almost all genera of legumes and the much-updated list of generic occurrences (and species occurrences for polymorphic genera) of EFNs across the family (Table 1). Taken at face value, these phylogenetic reconstructions suggest that the ancestral legume lacked EFNs and that EFNs first evolved in subfamily Caesalpinioideae in the early to mid-Eocene and have been prevalent in certain legume clades throughout most of the Cenozoic. However, the ancestral condition in legumes should be further evaluated using data spanning outgroups at least across Fabales where EFNs are known to occur in several genera of Polygalaceae (Eriksen and Persson 2007). Our reconstruction also shows that the evolution of EFNs in legumes substantially predates the evolution of the various legume myrmecophyte lineages, which arose much later in the mid- to late Miocene (Chomicki and Renner 2015), and also significantly predates the multiple origins of EFNs in subfamily Papilionoideae, which all date from the Miocene (Fig. 2). The phylogeny also suggests multiple independent origins of EFNs across legumes as a whole, depicting a pattern of clustered homoplasy for this trait within the legume family, a pattern that is further accentuated by multiple evolutionary losses in certain clades, such as at least four times within the mimosoid clade (see Caesalpinioideae above).

One explanation for such a pattern of clustered homoplasy is the evolution of cryptic precursor traits (genetic or developmental), as suggested by Marazzi *et al*. (2012). In the analysis of Marazzi *et al*. (2012), the precursor model explained the phylogenetic diversity of elevated parenchymatic EFNs significantly better than did conventional models of character evolution, and performed equally well in the case of the other, less specialised EFNs. Therefore, although it is entirely possible that at least some legumes are in some way predisposed to evolve EFNs, as suggested by Marazzi *et al*. (2012), it is also possible that the relative ease of evolving an EFN may mean that no cryptic precursor is required to prompt many independent origins, as depicted in Fig. 2. Indeed, growing knowledge of the diversity of legume EFNs (in terms of topographic locations on the plant, morphology, anatomy and inferred functional significance; Tables 3, 4) casts doubt on the homology of the full gamut of EFNs that are not topographically correspondent, nor structurally, anatomically or morphologically similar structures, but rather represent a set of non-homologous structures that are functionally broadly convergent, as observed at higher taxonomic scales (Weber and Keeler 2013). Clearly, homology assessment of legume EFNs is far from straightforward, but given the non-homology of, for example, parenchymatic EFNs on leaves of Caesalpinioideae and Detarioideae and trichomatic and abscission-zone EFNs in Papilionoideae, a precursor model to explain the full diversity of legume EFNs seems perhaps less compelling than it is for, for example, parenchymatic EFNs alone, where the occurrences across many lineages of Detarioideae, most Caesalpinioideae and a few early diverging lineages of Papilionoideae are more suggestive of a precursor, or even a scenario of a single gain of EFNs deeper in the phylogeny and massive losses within legumes, as has recently been proposed for the evolution of nodulation (van Velzen *et al*. 2019).

Such scenarios demand further testing but suggest that the complex evolutionary history of EFNs in Leguminosae may better be interpreted in terms of a set of distinct EFN evolutionary trajectories, some potentially with and some without cryptic precursors, some undergoing significant rapid and repeated disparification, and others disappearing in the form of evolutionary losses. In this regard, the possible role that EFN-bearing organs themselves may play in shaping the evolutionary trajectories of legume EFNs, including the morphological disparification of EFNs and evolutionary losses, should not be underestimated. Disparification can be interpreted in terms of the idea of individualisation (Marazzi *et al*. 2013*b*), whereas losses could have been precipitated as a ‘by-product’ of sudden or gradual evolutionary changes in the *Bauplan* of the EFN-bearing organ, which may occur independently from positive selection experienced by the EFNs. Such ‘accidental’ losses are perhaps more likely than are losses resulting from a negative selection on EFNs, because EFNs appear cheap to produce (O’Dowd 1979; see also Rosenzweig 2002) and are likely to persist by genetic or phylogenetic inertia even in the absence of mutualistic interactions (Pemberton 1998; Nogueira *et al*. 2012).

On another level, phylogenetic patterns with respect to where on a plant EFNs develop are also apparent in that the location of EFNs itself is far from random. The idea that EFNs on non-reproductive structures (e.g. leaves and stems) are associated with long-lived woody perennials and EFNs on reproductive structures (e.g. inflorescences, bracts and bracteoles) are more prevalent on short-lived herbaceous plants (Mckey 1989) is strongly borne out by our results (Table 3, Fig. 2). EFNs are prevalent on leaves and other non-reproductive organs across Detarioideae and the mimosoid clade of Caesalpinioideae (almost all genera bear EFNs on vegetative parts only), which are almost all long-lived woody perennials. In contrast, in papilionoids, EFNs are prevalent on inflorescences (30–46 genera bear EFNs on reproductive structures only) and, especially, almost exclusively in tribe Phaseoleae, which comprises mainly shorter-lived climbing herbs, lianas or scandent shrubs (Lewis *et al*. 2005), and in the genus *Vicia*, all of which are short-lived herbaceous species. Interestingly, the isolated elevated parenchymatic EFNs on leaves of early diverging Papilionoideae lineages also occur in genera that comprise long-lived perennial trees up to 25 m tall, adding further support to Mckey’s (1989) hypothesis. Comparative ecological studies are necessary to test this hypothesis and understand whether these fundamentally different protective strategies associated with these distinct life-history strategies (i.e. vegetative *v*. reproductive plant parts) are matched by differences in the kind of herbivory damage suffered (e.g. leaf herbivory *v*. florivory or seed predation).

Conclusions and future directions

Several legume EFN questions and issues requiring further work have been highlighted throughout this paper. First, it is clear that EFNs in several legume clades remain poorly known and very likely incompletely documented, most notably in subfamilies Cercidoideae and Detarioideae, where EFNs are inconspicuous and not easily detected without careful and sustained observation in the field. In many cases, EFNs are barely visible on herbarium specimens. Furthermore, because herbarium specimens usually consist of fertile material with mature foliage, younger foliage and their associated caduceus stipules where EFNs are most active are often not included. Second, more detailed reconstructions of the evolutionary history of EFNs across legumes could prove productive at several levels, including within Caesalpinioideae using species-level data and a more resolved phylogeny, but also across legumes as a whole, including a range of legume outgroups and considering early diverging papilionoid lineages where elevated EFNs are found. Such analyses could shed light on whether absence of elevated EFNs in Papilionoideae reflects a loss early in the evolutionary history of the subfamily and, hence, why Papilionoideae did not develop elevated EFNs in more taxa. Third, as our knowledge of EFNs in legumes increases, there is scope to examine the broad-scale geographic distribution and environmental (e.g. bioclimatic, fire) correlates of EFN occurrence and abundance for the first time. It is clear that EFNs in legumes are strongly concentrated in tropical lineages, with there being few examples of temperate legumes with EFNs (in line with patterns for myrmecophytes across angiosperms more generally; see Chomicki and Renner 2015); however, within the tropics, it is unclear whether EFN-bearing legumes are equally abundant across savannas, rain forests and seasonally dry tropical forests, or even deserts. These questions set the stage for exciting future research on legume EFNs in the coming years.

Conflicts of interest

C. E. Hughes is also an Associate Editor of the ‘Advances in Legume Systematics 13’ special issue. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Systematic Botany* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors have no further conflicts of interest to declare.

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