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REVIEW ARTICLE **Open Access**

A review for the pollinators of Papilionaceous flowers

Kelebek şeklinde çiçek açan çiçeklerin tozlayıcıları için bir inceleme

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ABSTRACT

The evolution of keel flowers within Fabaceae, Polygalaceae and some other clades of angiosperms is attributed to skilled and strong bees. However, whether this is true or not, is still an open question. Therefore, the literature is surveyed for the Hymenopteran pollinators of keel flowers, for 119 sources and for 112 species, six genera and two tribes for five characters which are the size of the flowers, Hymenopteran flower visitors/pollinators, size of the Hymenopteran pollinators, pollen and nectar robbers/thieves and size of the Hymenopteran thieves/robbers. The results suggest that Fabales keel flowers are mainly pollinated by long-tongued bees, from Apidae and Megachilidae families; and the most common pollinators of the keel flowers are small *Megachile* and *Osmia*; medium-sized *Apis, Anthophora* and *Eucera;* and large *Xylocopa*, *Bombus* and *Centris*. While the literature suggests that keel flowers are pollinated by skilled and strong bees, the results of the current review have shown that this is not the whole case in terms of flower size and bee size. There is no difference between pollinator diversity and flower size. While floral robbers/thieves are mostly up to 2 cm, among them honey-bees (*Apis mellifera*) both pollinate and rob the keel flowers. Keel flowers of Polygalaceae and other angiosperm lineages are somehow similar to the keel flowers of Papilionoideae.

ÖZ

Baklagil çiçek tipinin Fabaceae, Polygalaceae ve diğer angiosperm gruplarındaki evriminin becerikli ve güçlü arılar sayesinde olduğu fikri ortaya atılmıştır. Ancak, bunun doğruluğu tartışmalıdır. Bu nedenle, bu derlemede toplam 119 kaynak (112 tür, altı cins ve iki tribe) beş karakter (çiçek büyüklüğü, Hymenoptoran polinatörleri, Hymenoptoran polinatörlerinin büyüklüğü, polen ve nektar hırsızları, Hymenoptoran polen ve nektar hırsızlarının büyüklüğü) açısından değerlendirilmiştir. Derlemenin sonuçları göstermiştir ki, Fabales baklagil çiçekleri temelde Apidae and Megachilidae familyalarından uzun dilli arılar ile döllenmekte, ve en yaygın polinatörler ise küçük *Megachile* ve *Osmia*; orta boylu *Apis*, *Anthophora* ve *Eucera*; ve büyük *Xylocopa*, *Bombus* ve *Centris*'dir. Literatur, baklagil çiçeklerinin becerikli ve büyük arılarla döllendiğini önerirken, bu derlemenin sonuçları çiçek ve polinatör büyüklüğü açısından bunun tam anlamıyla doğru olmadığını göstermiştir. Ayrıca, çiçek büyüklüğü ve polinatör çeşitliliği arasında da bir bağlantı görülmemiştir. Çiçek hırsızları genelde 2 cm'ye kadar olurken, bunların arasında bal arılarının (*Apis mellifera*) hem hırsız hem de polinatör olarak işlev gördüğü anlaşılmıştır. Diğer taraftan, Polygalaceae ve diğer angiosperm baklagil benzeri çiçeklerin gerçek baklagil çiçeklerine polinatör açısından benzer olduğu görülmüştür.

1. INTRODUCTION

Keel flowers (Westerkamp, 1997) or papilionateous flowers are bilaterally symmetrical (in most cases), pentamerous flowers with the reproductive organs enclosed by keel petals (Polhill & Raven, 1981; Endress, 1994; Westerkamp, 1997; Pennington et al., 2000; Persson, 2001; Tucker, 2002; Tucker, 2003; McMahon & Hufford, 2005; Westerkamp & Claßen-Bockhoff, 2007; Bello et al., 2010). Keel flowers are dominant in two species-rich lineages within Fabales Bromhead, tribe Polygaleae Chodat of Polygalaceae family and subfamily Papilionoideae of Leguminosae family (Bello et al., 2007; Bello et al., 2010). While subfamily Papilionoideae with ca. 14,000 species in 504 genera constitutes almost 72% of species richness of family Leguminosae (Tucker, 2003; Lewis, 2005; LPWG, 2017), similarly tribe Polygaleae with ca. 800 spp. holds 80% of the species richness of the

Polygalaceae family (Persson, 2001; Bello et al., 2010; Bello et al., 2012).

Keel flowers are also found outside of Papilionoideae, in Cercidoideae, Dialioideae and Caesalpinioideae: *Cercis* L., *Poeppigia procera* C.Presl and *Peltophorum* (Vogel) Benth. (Arroyo, 1981; Polhill et al., 1981); and in many unrelated families, such as Ranunculaceae (*e.g.*, *Aconitum* L.), Hippocastanaceae (now a polyphyletic group), Geraniaceae (*e.g.*, *Pelargonium rapaceum* (L.) L'Hér.), Solanaceae (*e.g.*, *Schizanthus* Ruiz& Pav.), Campanulaceae (*e.g.*, *Monopsis lutea* (L.) Urb.), Fumariaceae (now subfamily Fumarioideae) (*e.g.*, *Corydalis cava* (L.) Schweigg & Körte), Plantaginaceae (*e.g.*, *Collinsia* Nutt.), Calceolariaceae (*e.g.*, *Calceolaria* L.), Strelitziaceae (*e.g.*, *Strelitzia reginae* Banks), Onagraceae, Trigoniaceae, Tropaeolaceae, Acanthaceae and Commelinaceae (Westerkamp, 1997). Indeed, it was suggested that keel flowers evolved at least 16 times within 10 different angiosperms orders, both in monocots and eudicots (Westerkamp, 1997). However, excepting Trigoniaceae and Fumarioideae, existence of keel flowers in other angiosperm families is not as extensive (*i.e.*, as number of species) as in Fabales (Westerkamp, 1997; Westerkamp & Weber, 1997). Particularly, *Cercis* is well known by its "pseudo-papilionoid" flowers with a bilaterally symmetrical corolla, and three different petal types: standard, wings and keels (Polhill et al., 1981). However, *Cercis* lacks some floral characteristics, such as connected stamens, and the tripping mechanism seen in most Papilionoideae flowers (Tucker, 2002).

Until now, many possible causes have been reported for the evolution of keel flowers such as a bigger display area (mainly the standard) and protection of ovarium and stamens from environmental factors such as rain, strong wind, high temperatures and evaporation (Breteler & Smissaert-Houwing, 1977; Polhill & Raven, 1981; Westerkamp & Claßen-Bockhoff, 2007; Shi et al., 2010; Etcheverry & Vogel, 2018). However, the most widely accepted view for the evolution of complex flowers such as keel and bilabiate flowers is an "adaptive response" to bees; keel flowers may have evolved to attract bees and/or to protect the flower from pollen robbery (*i.e.*, nectar/pollen stealers, pollen eaters and occasional visitors) (Leppik, 1966; Faegri & van der Pijl, 1979; Arroyo, 1981; Polhill et al., 1981; Brantjes, 1982; Schrire, 1989; Westerkamp, 1989; Howell et al., 1993; Proctor et al., 1996; Westerkamp, 1996; Westerkamp, 1997; Westerkamp & Weber, 1999; Fenster et al., 2004; Westerkamp & Claßen-Bockhoff, 2007; Etcheverry & Vogel, 2018). Pollen is hidden in the deepest part of the flower by the keel petals to secure pollination and promote cross-pollination, where pollen cannot be easily removed during grooming (Brantjes, 1982; Lloyd & Schoen, 1992; Westerkamp, 1996; Westerkamp, 1997; Zhang et al., 2011). Therefore, this particular adaptation has driven the evolution of keel flowers across several angiosperm groups, and keel flowers are not unique to Fabales, similar to other melittophilous (i.e., bee pollinated) complex flowers; they are widely distributed in many more angiosperm orders (Faegri & van der Pijl 1979; Westerkamp, 1997; Hingston & McQuillan, 2000; Etcheverry & Vogel, 2018).

While there are many pollination biology studies on the keel flowers (mainly Papilionoideae), an explicit study on the pollinators of keel flowers has never been performed until now. Such a study would be useful in clarifying the main bee pollinators of the keel flowers. The literature suggests that keel flowers are pollinated by skilled and strong bees, but which skilled/strong bees? Is large *Bombus* pollination more common than large *Centris* or *Xylocopa* Latreille pollination? Is there a difference among Papilionoideae keel flowers, Polygalaceae keel flowers, and Scrophulariaceae (*i.e.*, *Collinsia*) keel flowers in terms of their pollinators? Therefore, the first aim of the current study is to synthesize information on the pollinators of keel flowers.

On the other hand, flower size is frequently reported to be an important part of floral constancy related to searching time and pollinator attraction (Conner & Rush, 1996; Chittka et al., 1999; Goulson, 1999; Stout, 2000; Spaethe et al., 2001; Gegear, 2005; Gegear & Laverty, 2005; Skorupski et al., 2006; Benitez-Vieyra et al., 2007; Galloni et al., 2008; Lihoreau et al., 2016). Pollinator size also reported to be correlated to flower size (Gottsberger & Gottsberger, 1988; Galloni et al., 2008), pollen placement (Elle & Carney, 2003) and pollination success (Cristofolini et al., 2012). The literature on the effect of pollinator/flower size is case-dependent: while one study reports that large flowers are worked by only large bees and small flowers are pollinated by all sizes of bees (*e.g.*, Herrera, 2001), another study suggests that flower size and pollinator size are mostly correlated in which large flowers are pollinated by large bees, and small flowers are pollinated by small bees (*e.g.*, Gottsberger & Gottsberger, 1988). Thus, whether floral size and pollinator size are important criteria for the pollinators of keel flowers has never been explicitly addressed until now. While, employing field observations on this issue is possible, an easier way to gather this information would be through reviewing existing literature, published articles which is particularly prevalent for Papilionoideae (Leguminosae). Therefore, the second aim of the current review is to investigate pollinators of keel flowers within angiosperms in detail, to answer the questions below represent a subset of the questions were introduced above: Is there an overall size difference among pollinators of small and large keel flowers? Are small keel flowers pollinated by large bees too? Are medium-sized honeybees really robbers/thieves of keel flowers? To answer these questions and provide an overview of the pollinators of angiosperm keel flowers, a comprehensive literature review is performed.

2. MATERIALS AND METHODS

Between 2018 and 2019, the literature for information on the Hymenopteran pollinators of keel flowers was surveyed, for 119 sources and for 112 species, six genera (*Chamaecrista* (L.) Moench, *Cassia* L*.,* *Senna* Mill. Leguminosae; *Monnina* Ruiz&Pav*.,* Polygalaceae; *Collinsia*, *Penstemon* Schmidel*,* Plantaginaceae) and two tribes: *Crotalarieae* (Benth. Hutch) and Genisteae (Bronn) Dumort, Leguminosae; for five characters which are the size of the flowers, Hymenopteran flower visitors/pollinators, size of the Hymenopteran pollinators, pollen and nectar robbers/thieves and size of the Hymenopteran thieves/robbers (please see detailed information below on how characters were defined and included in the analysis). Other type of animal pollination studies (*e.g*., bird pollination, wasp pollination) are excluded.

Most of the studies reviewed here do not report the size of the bee visitors and studied flowers. Therefore, in these cases the flower and bee size data were obtained from alternative sources, such as, other published studies or suitable internet sources. In some cases, instead of the flower size, petal (corolla), standard (banner, flag) or keel size is given, and in these cases these sizes were accepted as the minimum flower size for simplicity. If the body size of a bee species/subspecies/variations could not be found, the body size of the species or genus was accepted to make approximate estimations. Non-bee visitors were not included in the visitor/pollinator column, because in some cases, instead of giving the species name of the wasps (Vespidae Latreille), hoverflies (Syrphidae Latreille), butterflies (Lepidoptera Linnaeus), flies (Diptera Linnaeus), beetles (Coleoptera Linnaeus), ants (Formicidae Latreille) among others, only the common name (*e.g*., flies) or the name of the order (*e.g*., Diptera) or the family name (*e.g*., Vespidae) is given. For brevity, where multiple sources present the same information, this information was not repeated while all appropriate citations are made.

Data is compiled in Supplementary Table 1. This table includes 106 entries from 119 studies which reported floral visitors, in some cases possible pollinators and nectar/pollen thieves of the keel flowers of Papilionoideae and Polygalaceae in Fabales, keel flowers outside of Polygalaceae and Papilionoideae, but still in Fabales (*i.e*., Cercidoideae), keel-flowers outside of Fabales (Ranunculales Juss. ex Bercht. & J.Pres and Lamiales), and some taxa which have non-keeled flowers from Papilionoideae (Fabales), Caesalpinioideae (Fabales) and Detarioideae (Fabales). These non-keeled flowered taxa and their pollinators/ robbers were included to the study just for comparison (to detect whether these flowers are pollinated with similar suits of pollinators of the keel flowers). Rows were numbered and listed according to flower type (1 to 95 keel flowers and 95 to 106 non-keeled flowers) and phylogeny (1 to 89 keel flowers of Fabales and 89 to 95 keel flowers outside of Fabales). The Hymenopteran pollinators were approached at the genus level.

In many studies, the most common visitors are accepted as the most effective pollinators; however, visitation frequency can be misleading and least common visitors can be more effective pollinators (Fenster et al., 2004). For instance, large flowers of *Collaea cipoensis* Fortunato visited by nectar-robbers (83%), nectar-thieves (9%), florivores (flower-eaters) (1%) and possible pollinators (only 3%) (Gelvez-Zuniga et al., 2018). Similarly, among 24 different species of visitors, only four of them were reported to be the effective pollinators of *Polygala vayredae* Costa (Castro et al., 2013). Therefore, a second table (Table 1) was constructed which includes only the studies in which possible nectar/pollen stealers as well as flower visitors and pollinators were distinguished. Flower visitors include all the categories: nectar/pollen stealers, nectar/pollen thieves, and pollinators.

In Table 1, 40 entries from 50 studies which reported floral visitors, possible pollinators and nectar/pollen stealers of the keel flowers of Polygalaceae (Fabales), Papilionoideae (Fabales), keel-flowers out of Fabales

(Ranunculales and Lamiales), and some of exemplar taxa which have non-keeled flowers (Papilionoideae and Caesalpinioideae) were included. In contrast to Supplementary Table 1, the species was numbered in this table to make following the results and discussion parts easier. However, similar to Supplementary Table 1, studies were listed according to their flower type (1 to 37 keel flowers and 37 to 40 non-keeled flowers), phylogeny (keel flowers of Fabales from 1 to 33 and keel flowers out of Fabales from 33 to 37) and flower size (1 to 7 flower sizes up to 1.2 cm, 7 to 37 flower sizes larger than 1.2 cm. From now on, both the results and the discussion will be based on this table which includes only the studies that reported not only all Hymenopteran visitors but also the legitimate pollinators and pollen/nectar stealers of the studied species.

Table 1. Fifty studies which reported floral visitors, possible pollinators and nectar/pollen robbers/thieves of the keel flowers of angiosperms. Name of the plant, size of the flowers, bee visitors and range of their sizes, nectar/pollen stealers (if given), size range of the Hymenopteran thieves, and the source(s) were indicated in separate columns. The sizes of both flowers and bees were given as centimetres (cm), and this information was found from proper sources, if it was not stated in the original study. The bee size range includes females, queens, males and workers in some cases. For the Hymenopteran visitors, if the percentage of visits or number of visits were given in the source, they were indicated within brackets. If the flower size could not be found, petal (corolla), standard (banner, flag) or keel size is given, and in these cases these sizes were accepted as the minimum flower size. Study areas were not indicated. Keeled flowers from Lamiales and Ranunculales families, and representative flowers of non-keeled Fabales are indicated. Same information from various sources is not repeated."/" and ";" represent different sources or information about different species. Question marks (?) indicate the information is not certain. Decimals are rounded to the nearest whole number to avoid fractional points. Empty cells represent unavailable information.

Name of the plant	Size of the flowers	Hymenopteran flower visitors /pollinators	Size range of Hymenopteran pollinators (cm)	Hymenopteran pollen and nectar robbers /thieves	Size range of robber /thieves (cm)	Source
1-*Apios americana*	0.1 cm	Flies are possible pollinators (but not confirmed), *Megachile* spp.	0.7-1.2 cm	*Apis mellifera, Lasioglossum* sp., Halictidae (?)	0.3-1.2 cm	Bruneau & Anderson, 1988; Westerkamp & Paul, 1993; Bruneau & Anderson, 1994
2-*Aeschynomene amorphoides*	0.43 cm	*Tetraloniella jaliscoensis*	About 1 cm	*Apis mellifera, Trigona fulviventris*, wasps, ants, some Lepidoptera and Coleoptera	0.5-1.2 cm	Carleial et al., 2015
3-*Polygala monticola* (Syn. *Polygala violacea*) (Polygalaceae)	About 0.5 cm	*Apis africana* hybrid (the most frequent visitor), *Megachile* sp., *Coelioxys* sp., *Exomalopsis* sp. (all activated the pollination mechanism)	0.7-1.2 cm	*Ceratina* sp.	Up to 0.8 cm	Brantjes, 1982
4-*Pultenaea villosa*	Corolla 0.6 cm	*Apis mellifera* (54%), *Lipotriches* spp., *Lasioglossum convexum, Trigona carbonaria*, unknown solitary bees, *Hyleoides* sp.	0.3-1.7 cm	Vespidae, Formicidae, Buprestidae, Chrysomelidae, Bombyliidae, Muscidae, Syrphidae, Heteroptera		Ogilvie et al., 2009
5-*Polygala vauthieri* (Polygalaceae)	About 0.7 cm	*Apis africana* hybrid (the most frequent visitor), *Megachile* sp., *Hypanthidium* sp. (all activated the pollination mechanism)	0.7-1.2 cm or larger	*Ceratina* sp., *Melissodes* sp.	0.8-1.8 cm	Brantjes, 1982

Name of the plant	**Size of the flowers**	**Hymenopteran flower visitors /pollinators**	**Size range of Hymenopteran pollinators (cm)**	**Hymenopteran pollen and nectar robbers /thieves**	**Size range of robber /thieves (cm)**	**Source**
6-*Anthyllis vulneraria subsp. vulgaris* (Syn. *Anthyllis vulneraria* subsp. *carpatica*)	0.7-1.2 cm	*Anthophora acervorum* (=*A. plumipes*) (45%), *A. robusta* (2%), *Andrena fulva* (3%), *Eucera longicornis* (2.4%), *Melecta luctuosa* (1%), *Megachile* sp. (1%),	0.7-1.7 cm	*Bombus terrestris* and *B. jonellus* (45%) (nectar robbers)	1.1-2.2 cm?	Navarro, 2000
7/8-*Vigna longifolia, V. luteola*	Standard 1.4-2.2 cm and 1.3-2.5 cm, respectively	*Bombus morio, Megachile susurrans, M. tenuitarsis, Xylocopa brasilianorum* (these four are the most important pollinators), *Apis mellifera, Centris decolorata, C. tarsata, Coelioxys* sp., *Eufriesea mussitans, Pseudaugochlora* sp., *Xylocopa frontalis, Exomalopsis analis*	0.7-3 cm	Lepidoptera, Diptera, Coleoptera		de Souza et al., 2017
9-*Crotalaria juncea*	Keel 1.5 cm	Large *Megachilid* bees, *Megachile sculpturalis, Xylocopa, Xylocopa virginica* and *X. micans*	1.2-2.7 cm	*Apis mellifera*	About 1.2 cm	Hall & Avila, 2016
10-*Lupinus perennis*	About 1.5 cm	*Bombus* spp., solitary bees (mostly *Osmia*, *Andrena vieina, Megachile melanophaea melanophaea*), *A. mellifera, Xylocopa virginica*	0.5-2.3 cm	Small bees, wasps, butterflies and hummingbirds		Bernhardt et al., 2008
11-*Pongamia pinnata*	1.5-1.8 cm	*Apis dorsata, A. cerana indica, A. florea* (in total ~70%) *Amegilla* sp. (~10%), *Megachile* sp. (~5%), *Xylocopa latipes* and *X. pubescens* (~10%)	0.7-3.5 cm	*Trigona iridipennis, Ceratina simillima, Pithitis binghami* (pollen thieves)	0.4-1.8 cm	Raju & Rao, 2016
12-*Polygala vayredae* (Polygalaceae)	About 1.6 cm	*Bombus pascuorum* (17%), *Anthophora* sp (5%) (both main pollinators), *Eucera longicornis, Halictus* sp.	0.8-1.7 cm	*Bombus terrestris* (64%), *B. pratorum* (both are nectar robbers); *Apis mellifera* (nectar thieves)	1.1-1.7 cm	Castro et al., 2008a, Castro et al., 2008b; Castro et al., 2013
13-*Bowdichia virgilioides*	1.75 cm	*Centris aenea* (main visitor), *C. fuscata* (main visitor) *Xylocopa* sp., *Apis mellifera, Trigona* spp., *Partamona* sp., *Geotrigona* sp. (all occasional visitors)	0.3-3 cm	Vespidae, Braconidae, Lepidoptera, Hesperidae,		Gomes da Silva et al., 2011
14-*Lathyrus japonicus*	Standard 1.8-2.3 cm	*Bombus pascuorum, B. lapidarus, B. hortorum, B. terrestris, Osmia* sp.	0.6-2.2 cm	*B. terrestris* workers (nectar robber/thief), *Apis mellifera, Coelioxys* (nectar thief)	0.7-1.7 cm	Asmussen, 1993

Name of the plant	Size of the flowers	Hymenopteran flower visitors /pollinators	Size range of Hymenopteran pollinators (cm)	Hymenopteran pollen and nectar robbers /thieves	Size range of robber /thieves (cm)	Source
15-*Coronilla emerus* (Syn. *Hippocrepis emerus*)	About 2 cm	*Eucera* is the most important pollinator, other than *Habropoda Osmia, Xylocopa, Bombus, Antophora* sp., *Megachile* sp.	0.6-2.6 cm	*Apis mellifera, Bombus sp.,* Halictae	0.4-2.3 cm	Galloni et al., 2008; Aronne et al., 2012
16-*Crotalaria retusa*	Flag 2 cm	*Xylocopa frontalis* (49%) *X. grisescens* (44%), *Centris leprieuri*	2.9-3 cm	*Trigona spinipes* (nectar robber)	0.5-0.7 cm	Jacobi et al., 2005
17-*Crotalaria micans*	2-2.5 cm	*Pseudocentron* (*Megachile*) sp. (the most effective pollinator), *Xylocopa macrops, X. ordinaria, X. eximia*	0.7-2.6 cm	*Apis mellifera* and *Bombus morio* (nectar thieves)	1.2-2.5 cm	Etcheverry et al., 2003
18-*Lupinus pilosus*	2-2.5 cm	*Apis mellifera, Antophora* sp. (both activated the tripping mechanism)	0.8-1.6 cm	Small solitary bees	0.5-1.7 cm	Ne'eman & Nesher, 1995
19/20-*Cratylia hypargyrea, C. mollis*	About 2.5 cm	Five *Xylocopa* and four *Centris* species	1.2-3 cm	Some bees are too small to pollinate the flowers		Queiroz, 1996
21-*Robinia pseudoacacia*	About 2.5 cm	*Apis mellifera* (63%)	About 1.2 cm	*Apis mellifera*	About 1.2 cm	Giovanetti & Aronne, 2012
22-*Cytisus scoparius*	2-3 cm	*Apis mellifera, Andrena, Anthophora, Bombus*, one solitary bee, *Osmia, Tetralonia nipponensis, Xylocopa appendiculata circumvolans, Campsomeriella annulata annualata, Lasioglossum* spp., *Halictus acerarius, Bombus melanopygus* (10), *Lasioglossum pacificum* (4), and *Lasioglossum olympiae* (4), *Bombus mixtus, Andrena salicifloris, B. flavifrons, B. vosnesenskii, Evylaeus* sp.	0.3-2.3 cm	Small bees, *A. mellifera*	About 1.2 cm	Parker, 1997; Suzuki, 2000; Malo & Baonza, 2002; Parker et al., 2002; Galloni et al., 2008; Muir, 2013
23-*Collaea cipoensis*	Corolla 2-3 cm	*Apis mellifera, Xylocopa muscaria*	1.2-2.6 cm	*Trigona spinipes, Toxomerus musicus* (nectar robber bees), *Apis mellifera, Exomalopsis* sp., *Megachile* sp. *Melipona marginata, Augochloropsis* sp., *Ceratina* sp.	0.3-1.3 cm	Gélvez-Zúniga et al., 2018
24-*Periandra mediterranea*	Petals about 2.3 cm/standard 3.3 cm	*Xylocopa frontalis, Acanthopus excellens* and *Epicharis* sp. (both occasional visitors)	1.5-3 cm	*Apis mellifera, Acanthopus excellens, Epicharis* sp., *Polybia* spp (wasp), butterflies, hummingbirds	1.2-2.5 cm	Meireles et al., 2015

	Name of the plant	**Size of the flowers**	**Hymenopteran flower visitors /pollinators**	**Size range of Hymenopteran pollinators (cm)**	**Hymenopteran pollen and nectar robbers /thieves**	**Size range of robber /thieves (cm)**	**Source**
	25-*Canavalia virosa* (Syn. *Canavalia cathartica*)	Standard 2.7-3 cm	*Xylocopa flavorufa, Megachile combusta, Apis mellifera* (occasional visitor)	1.2-2 cm	Bees smaller than *Megachile combusta, Apis mellifera* / Small ants as nectar robbers	Less than 1.2 cm	Stirton, 1977; Sahai, 2009
	26-*Canavalia gladiata*	Standard 3.5 cm	*Apis mellifera* (occasional visitor)	About 1.2 cm	Small ants as nectar robbers		Sahai, 2009
	27-*Lathyrus latifolius*	Flag 3.3 cm	*Megachile ericetorum, Xylocopa violacea* and other megachilids as the main visitors	0.7-2.8 cm	*Apis mellifera*	About 1.2 cm	Westerkamp, 1993
	28-*Centrosema virginianum*	2.5-4 cm (petals 2.1-3.5 cm)	Mostly large bees. *Bombus pennsylvanicus, Xylocopa micans, Melissodes communis, Megachile campanulae wilmingtoni, Megachile policaris, Colletes distinctus*	0.8-2.7 cm	Coleoptera, Diptera, Lepidoptera, Othoptera are florivores or folivores		Cardel, 2004
	29/30-*Centrosema pubescens, C. brasilianum*	Banner 3.4 and 3.6 cm, respectively	*Euglossa*, *Eufriesea, Eulaema, Bombus brevivillus, Centris, Epischaris, Xylocopa, Acanthopus,* however *Euglossa cordota,* three *Eulaema* species, *Bombus brevivillus, Epicharis flava, Xylocopa frontalis* were the most common pollinators	up to 2 cm	*Oxaea, Ceratina, Augochloropsis, Ceratina, Pseudaugochlora, Exomalopsis, Centis, Epicharis*	up to 1.5 cm	Ramalho et al., 2014
	31-*Vicia faba*	3-4 cm	*Eucera pulveracea* (50%), *Apis mellifera* (42%)	1.2-1.6 cm	*Apis mellifera* (42%) (both pollinator and nectar robber), *Xylocopa violacea* (1.6%) (nectar robber)	1.2-3 cm	Aouar-Sadli et al., 2008
	32-*Vigna caracalla* (Syn. *Cochliasanthus caracalla*)	4.8 cm and 4-7 cm, respectively	*Bombus morio, Xylocopa eximia, Centris bicolor, Eufriesea mariana*	1.3-2.5 cm	*Apis mellifera, Meliponini* sp. (both small pollen robbers)	0.3-1.2 cm	Etcheverry et al., 2008; Etcheverry & Vogel, 2018
RANUNCULALES	33-*Aconitum napellus ssp. lusitanicum* (Ranunculales)	About 2 cm	Pollinated by long-tongued bumblebees, *Bombus pascuorum, B. terrestris*	About 1.7 cm	Honeybees (nectar robbers)	About 1.2 cm	Mayer et al., 2014

	Name of the plant	Size of the flowers	Hymenopteran flower visitors /pollinators	Size range of Hymenopteran pollinators (cm)	Hymenopteran pollen and nectar robbers /thieves	Size range of robber /thieves (cm)	Source
	34-*Corydalis cava* (Ranunculales)	2.35 cm	*Bombus terrestris* queens (the most important pollinator), *Anthophora acervorum*, *B. pratorum* and *B. hortorum* (both are rare)/Queens of *Bombus lucorum* and *B. cryptarum* (34%), *B. terrestris* (38%), *B. hortorum* (24%), *B. pratorum* (0.2%), *B. lapidarius* (0.5%), *Apis mellifera* (2%) (1.4%), *Anthophora plumipes* (1.4%)	1-2.2 cm	All *Bombus* species are also nectar robbers/ *Apis mellifera, Andrena, Nomada, Sphecodes*	0.4-2.3 cm	Olesen, 1996; Myczko et al., 2015
LAMIALES	35-*Collinsia sparsiflora* (Lamiales)	0.9-1.6 cm	*Apis mellifera, Bombus edwardsii, B. vosnesenskii, B. caliginosus, B. californicus, Synhalonia hurdi, S. lunata, S. edwardsii, Osmia lignaria, O. glauca, O. bruneri, O. bakeri, O. nemoris, Chelostomopsis ribifloris, Hoplitis fulgida, Lasioglossum* sp.	0.3-2.3 cm	Flies, moths, butterflies		Rust & Clement, 1977
	36-*Collinsia* spp. (Lamiales)	0.4-1.7 cm	*Bombus, Osmia, Anthophora, Emphoropsis, Synhalonia,* long-tongued bees/ *Apis mellifera*, short-tongued bees	0.9-1.9 cm	Flies moths, butterflies, short-tongued bees		Armbruster, 1980; Kampny, 1995; Armbruster et al., 2002
NON-KEELED FLOWERS OF FABALES	37-*Amorpha canescens* (non-keeled, Papilionoideae)	Banner 0.5-0.6 cm	Solitary bees, *Lasioglossum* (*Dialictus* and *Evylaeus*), Honeybees, *Andrena quintilis, Calliopsis andreniformis, Colletes robertsonii*	0.3-1.7 cm	Syrphid flies	1-1.2 cm	Slagle & Hendrix, 2009
	38-*Caesalpinia echinata* (non-keeled, Caesalpinioideae)	About 2.5 cm	The most effective pollinators are medium-sized to large bees (larger than 1.2 cm). *Apis mellifera*, *Centris aenea, C. analis, Xylocopa frontalis, X. grisescens*, and *X. suspecta*	1.2-3 cm	*Trigona spinipes, Trigona* sp., *Augochlora* sp., *Pseudaugochlora* sp.	0.3-1.3 cm	Borges et al., 2009
	39-*Chamaecrista chamaecristoides* (non-keeled, Caesalpinioideae)	3 cm?	Only large insects such as *Xylocopa, Eufriesea, Eulaema, Euglossa* and *Ptiloglossa* contact and vibrate sexual organs	1.1-2.7 cm	*Apis mellifera, Florilegus* sp., *Protoxaea* sp., *Exomalopsis* sp.	0.8-1.2 cm	Arceo-Gómez et al., 2012

Name of the plant	Size of the flowers	Hymenopteran flower visitors /pollinators	Size range of Hymenopteran pollinators (cm)	Hymenopteran pollen and nectar robbers /thieves	Size range of robber /thieves (cm)	Source
40-*Cassia, Chamaecrista, Senna* (non-keeled *Cassia*/Senna and with a keel like petal *Chamaecrista;* Caesalpinioideae)	*Chamaecrista* petals to 1-2 cm or more/*Cassia* up to 6 cm, *Senna* up to 5 cm	Mainly large bees, *Xylocopa*, *Centris,* *Epicharis,* *Exomolopsis,* *Bombus,* *Euglossa,* *Augochloropsis,* *Pseudaugochloropsis,* *Ptiloglossa,* *Florilegus,* dependent on the flower size some small bees; large *Oxaea,*	0.8-3 cm	*Oxaea flavescens, Pseudaugochloropsis, Trigona*	up to 1.5 cm	Gottsberger & Gottsberger, 1988; Dulberger et al., 1994

3. RESULTS

Both Table 1 and Supplementary Table 1 show that Fabales keel flowers are mostly pollinated by long-tongued bees, Apidae L. and Megachilidae families, but rarely by Andrenidae (*Andrena* Fabricius*),* Halictidae Thomson (*Lasioglossum* Curtis*, Halictus* Latreille*, Pseudaugochlora* Michener*, Lipotriches* Gerstaecker), Colletidae Lepeletier (*Colletes* Latreille), flies, wasps, birds and other animals, such as rodents. These last animals (not Hymenopteran) are not included in any of the two tables.

The most common pollinators of the keel flowers at the genus level are *Xylocopa* (19 spp. of keel flowers), *Apis* Linnaeus (16 spp.), *Megachile* Latreille (14 spp.), *Bombus* (13 spp.), *Centris* (8 spp.), *Osmia* Panzer (5 spp.), *Anthophora* Latreille (4 spp.), *Eucera* Scopoli (4 spp.). Other pollinators were recorded for less than three plant species. In terms of bee body sizes, large bees such as *Bombus, Centris, Eufriesea and Xylocopa* visit almost always only large flowers measuring at least 1.3 cm length (however, note *Bombus* visits of smaller *Collinsia* flowers), the remaining bees (*e.g., Apis*, *Megachile, Anthophora*) visit all sizes of flowers (Table 1). Here, it is possible to interpret these results as the relative abundancy of large bee visits (up to 3 cm, *Xylocopa, Centris* and *Bombus*). The small (up to 1.2 cm, *Osmia* and *Megachile*) and medium-sized (up to 2 cm, *Apis, Antophora* and *Eucera*) bee visits are also not rare (*Apis and Megachile* visits for 16 species and 14 species of keel flowers, respectively).

In terms of flower sizes, seven studies (studies 1 to 6 and, 37, including two Polygalacae and one non-keeled-Papilionoideae studies) suggested that flowers with a size up to 1.2 cm are pollinated by bees with a size of 0.3-1.7 cm, but not larger than 1.7 cm. On the other hand, if the flower size is larger than 1.3 cm (including one Polygalacae study, four keel flowers out of Fabales and three non-keeled flower studies), the pollinator size varies (0.3-3.5 cm). However, it should be noted that the pollinator size of large flowers (0.3-3.5 cm) includes the pollinator size of small flowers (0.3-1.7 cm). There was no correlation between pollinator species diversity and flower size, other than these size differences.

Nectar/pollen thieves and robbers are from different insect groups such as (mostly) Hymenoptera, Lepidoptera and Heteroptera. The Hymenopteran robbers/thieves are generally up to 2 cm. *Bombus* and *Xylocopa* are reported to be robber/thief by only a few studies. Among the studies in which the thief/robber size are known (excepting taxa 4, 7, 8, 10, 13, 19, 20, 26, 28, 35, 36), for nine taxa (including one keel flowers out of Fabales and two non-keeled flower studies) the robber size is clearly smaller than the pollinator size (taxa 9, 16, 23, 24, 25, 32, 33, 38, 39). In the other studies, robber/thief size is within the pollinator size range. In six studies, the robber size is larger than the pollinator size, or almost equal (taxa 5, 6, 12, 17, 21, 31), while in the remaining 13 studies the robber size is somehow smaller than the pollinator size, but still within the range of pollinator size.

Out of 36 keel-flowered taxa (Table 1), for six taxa *Apis mellifera* Linnaeus is suggested as both pollinator and nectar-pollen thief/robber, for eight taxa honeybees are suggested as only pollinators, and for 11 taxa honeybees are reported to be only nectar/pollen thieves or robbers. According to these results, it is possible to conclude that if the flower size is larger than 2 cm, *A. mellifera* tends to be both pollinator and robber/thief (taxa 21, 22, 23, 25, 31 and 34), rarely only a pollinator (taxa 18 and 26). However, there were no keel flowers smaller than 2 cm to show this pattern. On the other hand, if the flower size is smaller than 2 cm, honeybees are able to pollinate the keel flowers (taxa 4, 7, 8, 10, 13, 35, 36).

Except *Hypanthidium* (Megachilinae), the Polygalaceae pollinators are not different from Papilonoideae pollinators. The pollinators/visitors of non-keeled flowers of Fabales and other keel flowered lineages are somehow different (Table 1). Other than some common pollinators such as *Apis, Anthophora, Bombus, Xylocopa, Centris, Eufriesia* Cockerell*, Eulaema* Lepeletier and *Euglossa* Latreille*;* these different pollinators/visitors are *Calliopsis* Smith (*Amorpha canescens* Pursh), *Ptiloglossa* Smith (*Chamaecrista*), *Augochloropsis* Cockerell (*Senna, Chamaecrista*), *Pseudaugochloropsis* Cockerell (*Senna*), *Chelostomopsis* Cockerell (*Collinsia sparsiflora* Fisch. & C. A. Mey.), *Emphoropsis* Ashmead (*Collinsia*), *Synhalonia* Patton (*Collinsia, Cercis canadensis* L.). However, in terms of size, the pollinators of non-Fabales keel flowers and non-keeled flowers compared to floral size, were not different from Papilonoideae pollinators.

4. DISCUSSION

4.1. Pollinators of keel flowers

Convergent floral traits among unrelated taxa driven by shared pollinators are referred as pollination syndromes *sensu* Faegri & van der Pijl (1979) (Armbruster, 1993; Ollerton & Watts, 2000; Johnson et al., 2003; Fenster et al., 2004; Johnson & Jürgens, 2010; Schiestl & Johnson, 2013). Many studies have attributed the evolution of keel flowers within Leguminosae, Polygalaceae and other clades of angiosperms to bees (Leppik, 1966; Westerkamp, 1989; Endress, 1994; Westerkamp, 1997; Westerkamp & Weber, 1999), but particularly to skilled and strong bees (Leppik, 1966; Faegri & van der Pijl, 1979; Westerkamp, 1997). Similar to the results of Hingston & McQuillan (2000), the current review supports that keel flowers are bee flowers (*i.e*., bee pollination syndrome), but particularly long-tongued bee (Apidae and Megachilidae) flowers. The dominance of long-tongued bee visitors was also significant in Robertson's (1928) classification. The most common genera of pollinators among these long-tongued bees are large *Xylocopa, Bombus, Centris*; small to medium *Apis, Megachile, Osmia, Anthophora* and *Eucera*, in which *Xylocopa, Bombus, Centris, Apis* and *Megachile* are by far the most common ones (Table 1).

While van der Pijl (1961) grouped large flowers as "*Xylocopa* pollinated large flowers", similarly Arroyo (1981) suggested that some papilionoid flowers are specialized to large bees such as *Centris* and *Xylocopa*. At first, it may seem appropriate that large bees are strong enough to trip the keel flowers and their hairy bodies match perfectly to the large-keel flowers' pollination (Heering, 1995; Shambhu, 2013), in addition to the occurrence of morphological obstacles such as thick petals, floral connections, wing sculptures on the large flowers to exclude small visitors to reach the pollen (Queiroz, 1996; Etcheverry et al., 2008; Etcheverry & Vogel, 2018). However, the current study suggests that while large bees prefer large flowers, small and medium-sized bees also visit and pollinate these large flowers, as well as they visit medium and small flowers. It should be noted that, these results contradict to Herrera (2001), who indicates that large flowers are worked by only large bees and small flowers are pollinated by all sizes of bees. Yet, in the correct review, in terms of bee body sizes, there was also evidence that large bees such as *Bombus, Centris, Xylocopa* and *Eufriesea* visit only large flowers which are larger than 1.3 cm, small-medium bees such as *Apis, Anthophora, Osmia, Eucera* and *Megachile* do not have a preference, they visit and pollinate both small, medium and large flowers. Moreover, in terms of flower sizes, this study has shown that while flowers up to 1.2 cm are pollinated by bees with a size of 0.3-1.7 cm, larger flowers are pollinated by all sizes of bees (0.3-3.5). Indeed, these results correspond to general trends which are large flowered species (>15 mm length) are pollinated by large bees), but also medium-sized *Osmia* (Megachilidae); medium-sized flowers (8-15 mm) are pollinated mostly by small-medium sized *Osmia* and small flowered species (<8mm) are pollinated by small *Osmia* and other very small bees (Scott Armbruster, personal observation). Therefore, in contrast to common belief, this review partly supports that keel flowers are pollinated particularly by skilled and strong bees (Leppik, 1966; Faegri & van der Pijl, 1979; Westerkamp, 1997); because, the results have clearly showed that keel flowers are not pollinated by only large and strong bees, only that large bees prefer large flowers.

The current literature review on the pollination biology of keel flowers showed that many bee species move freely between small and large flowers. In this case, it is possible that rather than only the bee size, other characteristics of the pollinators such as optimum size of the bees (Stout, 2000; Stanley et al., 2016; de Souza et al. 2017), strength (Córdoba & Cocucci, 2011), handling type (Stanley et al., 2016), constancy (Gumbert & Kunze, 1999; Gegear & Laverty, 2005), flower colour (Raine & Chittka, 2007; Peter & Johnson, 2008), bee fauna (Gross, 2001; Bernhardt et al., 2008), environmental conditions such as temperature (Parker et al., 2002) and pollination mechanisms of Papilionoideae (valve, pump, explosive and brush, *e.g.,* Westerkamp, 1997) may be also important or bee preferences. For example, it was observed that the legume-loving megachilids commonly move between both small and large *Collinsia* flowers at least if the flowers have somewhat similar colour and plants themselves can support their weight (Scott Armbruster, personal observation). Megachilids have a behaviour that allows them to depress the keel even when they are too small for their weight to do it. They brace their head/mandibles against the base of the flag and push with their legs. They pop the keel down very effectively despite their light weight. This allows a much broader range of bee sizes for any given flower size and vice versa (Scott Armbruster, personal observation). Similarly, Megachilide visit three sympatric coflorecent species of the *Crotalaria* genus, with a yellow corolla. *Bombus attratus* and *B. morio* visit *Cologania broussoneti, Desmodium uncinatum*, two legumes with magenta flowers, while visiting *Hyptis mutabilis* (Lamiaceae) and *Mimosa* sp. (Mimosoideae) in a Northwestern community of Argentina (Trinidad Figueroa & Angela Etcheverry, unpublished results).

On the other hand, while some studies reported that small-keel flowers are generally pollinated by different bee species and large flowers show the highest pollinator specificity with few large bee groups such as *Bombus* and *Xylocopa* (*e.g.*, Brantjes, 1982; Queiroz, 1996; Herrera, 2001; Galloni & Cristofolini, 2003; Jacobi et al., 2005; Cane, 2006; Hargreaves et al., 2009), there was no correlation between pollinator diversity and flower size, other than size differences of the bees. Aronne et al. (2012) reported similar results that bee species diversity and flower sizes were not related; however, they showed that an increase in flower sizes were certainly correlated to an increase in the pollination by large *Bombus*. It was not encountered that *Bombus* have pollinatated flowers which are less than 1.3 cm (Table 1). However, this also does not seem like a universal pattern (*e.g.,* Spaethe et al., 2001).

4.2. The situation of *Apis mellifera*

The efficiency of honey bees (*Apis meliifera*) is an interesting issue for the keel flowers. As nectar or pollen thieves/robbers, *A. mellifera* do not show a preference between different floral sizes. These results suggest that due to their medium size (about 1.2 cm), honeybees can pollinate small flowers (whatever their purpose is); however, they probably accidently pollinate larger flowers during stealing (*i.e*., beneficial effect of a robber, Maloof & Inouye, 2000). In this case, it is possible to relate this issue to the size of pollinators compared to the flower size which is very important for the fitness of a plant species in terms of the place of pollen deposition, tripping the mechanism and foraging behaviours (*i.e*., handling time, flying distances, visitation frequency) (Herrera, 2001; Vivarelli et al., 2011), because a mismatch between the flower and the pollinator may be result in nectar/pollen robbing or thieving (Hargreaves et al., 2009). Thus, I agree with Westerkamp (1991 and 1993), in which *A. mellifera* referred as “clumsy-poor pollinators; they learn by trial, they are active in all seasons including when there is little choice, and in these periods, they learn how to avoid from the blows that accompany explosive pollination, by collecting nectar without pollinating the flowers”. Actually, many studies have presented similar results which indicate honeybees as poor pollinators compared to their size (*e.g*., Henning et al., 1992; Eynard & Galetto, 2002; Córdoba & Cocucci, 2011; Aronne et al., 2012), however, they still are able to work on flowers of many different plant species (Córdoba & Cocucci, 2011).

4.3. The situation of Polygalaceae, other keel flowered lineages, and non-keeled Fabales flowers

The pollinators of Polygalaceae keel flowers are also similar to pollinators of the Papilionoideae keel flowers. On the other hand, some of exemplar non-keeled flowers of Leguminosae which are included to this review are visited by different Hymenopteran genera, in which some of them have never been reported for the keel flowers before. However, other factors such as the bee fauna of the area and the limited number of studies available may be the key factors on this issue. Therefore, further studies are needed to confirm whether all keel flowers are pollinated by similar suites of pollinators or not.

Gottsberger & Gottsberger (1988) stated that, in contrast to small-flowered and non-keeled *Chamaecrista* which is pollinated by mostly small bees; non-keeled but large *Cassia, Chamaecrista* and *Senna* are pollinated by large bees such as *Xylocopa*, *Centris, Epicharis* Klug and *Bombus*; small bees are too small to pollinate these flowers (*i.e.*, occasional pollinators or robbers). Interestingly, some small flowers of *Chamaecrista* which show corolla modifications are mostly visited by large bees. Similarly, Borges et al. (2009) stated that the non-keeled flowers of *Caesalpinia echinata* Lam. are pollinated by medium to large bees such as *Xylocopa, Centris* and *Apis mellifera*. Therefore, in general, while keel and non-keeled flowers of Leguminosae share some similar suit of floral visitors, still there are differences. Indeed, both *Senna*, *Chamaecrista* and *Cassia* show some characteristics of keel flowers (*i.e.*, a bilateral symmetry, partly enclosed reproductive organs by a tubular petal, petal differentiation), and this may explain these similar pollinators with the keel flowers. However, in this case, again, the bee fauna of the study area, floral size, odour, inflorescence size, colour among others may be the principal factors which effects pollinators' choice. Still, compared to generalist *Gentiana lutea* L. with more than 30 insect visitors (Rossi et al., 2014), not only keel flowers but also keel-like flowers of Leguminosae are clearly far from being generalist. Therefore, in contrast to Arroyo (1981), the pollinator specialization does not have to be with only one type of pollinator, having more than one pollinator with similar characteristics can also be an indicator of specialization (Fenster et al., 2004; Galloni et al. 2008; Cristofolini et al. 2012).

Similar to the Fabales keel flowers, *Collinsia heterophylla* Buist ex Graham (Lamiales), *Aconitum napellus ssp. lusitanicum* Rouy (Ranunculales) and *Corydalis cava* (Ranunculales) keel flowers were also reported to be specialized onto long-tongued bees (Rust & Clement, 1977; Armbruster, 1980; Kampny, 1995; Olesen, 1996; Armbruster et al., 2002; Fenster et al., 2004; Mayer et al., 2014; Myczko et al., 2015). Among them, similar to the Papilionoideae keel flowers, *Collinsia heterophylla* seems generalist at first; however, a close look revealed that this species is pollinated by only long-tongued bees of 14 different species (Armbruster, 1980; Fenster et al., 2004). For *Collinsia*, except a few long-tongued bees (*Chelostomopsis, Emphoropsis* and *Synhalonia*), most of the pollinators were common in Fabales keel flowers (*i.e.*, *Apis, Anthophora, Bombus, Xylocopa, Centris, Eufriesia, Eulaema* and *Euglossa*). Similarly, other than *Synhalonia* (which is a long-tongued bee and a common visitor of *Collinsia*), the visitors of *Cercis* were not different from the Papilionoideae keel flowers. Thus, in the light of these findings, it may be more appropriate to refer the keel flowers of not only Papilionoideae, but also all angiosperm keel flowers as "long-tongued bee specialized". Since Harder (1983) concluded that long-tongued bees are more efficient pollinators compared to the short-tongued bees with a similar size, keel flowers might be evolved to host these efficient pollinators, not only large and strong bees to take guarantied the pollination success (Galloni et al., 2008; Cristofolini et al., 2012).

4.4. Limitations of the current study and literature

There are some important caveats to this review. This study does not include all studies on the pollination biology of the keel flowers, instead a subset selection of studies approach was maintained. Similarly, since non-Hymenopteran pollination is not very common among keel flowers (Hingston & McQuillan, 2000), these studies (*e.g.*, bird pollination, wasp pollination) are excluded. Second, flowering phenology (Hingston, 1999), population density (Bernhardt et al., 2008; Hattori et al., 2015), floral size of the populations (Elle & Carney, 2003), inflorescence size (Parker et al., 2002; Bauer et al., 2017), pollination mechanisms (Galloni et al., 2008; Cristofolini et al., 2012), reward (nectar or pollen) (Galloni et al., 2008; Cristofolini et al., 2012), floral colour (Streinzer et al., 2009), floral height (Waddington, 1979; Dafni et al., 1997; Gumbert & Kunze, 1999; Spaethe et al., 2001; Valido et al., 2002; Rafferty & Ives, 2013), floral chamber (Amaral-Neto et al., 2015) among others are not included here, even though these characters are reported to be very important for pollinator attraction. Third, the Hymenopteran fauna where the studies were done and pollinator abundance/absence/behaviour are other important factors (Gross, 2001; Stout et al., 2002; Elle & Carney, 2003; Bernhardt et al., 2008; Pando et al., 2011; Rossi et al., 2014; Myczko et al., 2015) for any pollination study, and these were not included in the current review. For example, Kožuharova & Firmage (2009) and Castro et al. (2013) showed that number of visits of different pollinators, robbers and thieves changes from year to year and population to population, even between close plant populations. Similarly, *Apis mellifera* was the most important pollinator of *Collinsia sparsiflora* in one region, while the numbers were very low in other regions (Rust & Clement, 1977). Indeed, these differences could be related to plant community differences and co-occurring plant species, microclimates, geographic region, season, weather conditions, humidity, altitude, low temperatures, wind and habitat degradation (Armbruster, 1980; Asmussen, 1993; Primack & Inouye, 1993; Hingston & McQuillan, 2000; Malo & Baonza, 2002; Parker et al., 2002; Galloni & Cristofolini, 2003; Rodríguez-Riaño et al., 2004; Vivarelli et al., 2011; Castro et al., 2013). Fourth, pollinator efficiency and successful seed set may be a more reliable signifier of the pollination biology of species than visitation. For example, while it was observed that bees with similar sizes *Anthophora, Megachile, Eucera* and *Bombus* visit *Coronilla emerus* L. flowers, no pollen grains were found on *Bombus* and *Anthophora*, which indicates *Megachile* and *Eucera* were more efficient pollinators of *C. emerus* (Aronne et al., 2012). Similarly, Vivarelli et al. (2011) showed that even though *Ononis masquillierii* Bertol. flowers are mostly visited by small bees (83%), flowers visited by large bees yielded increased seed sets compared to the flowers which were visited by smaller bees, because probably small bees increase selfing by activating the pollination mechanism many times and larger bees can carry the pollen grains for longer distances. Even for the small flowers of *Desmodium incanum* DC., the pollen release was lower if the small bees activated the explosive pollination mechanism, compared to larger bees (Alemán et al., 2014). However, this information (*i.e.*, pollinator efficiency and successful seed set) was found rarely in the literature review. Fifth, strength (Westerkamp, 1993; Córdoba & Cocucci, 2011), tongue size (Ramalho et al., 2014) and pollinator fidelity (Cristofolini et al., 2012) are as important as the bee size in terms of keel flower pollination. For instance, *Megachile ericetorum* Lepeletier males were able to trigger the pollination mechanism of *Lathyrus latifolius* L. flowers, while similar sized *A. mellifera* cannot (Westerkamp, 1993). Lower fidelity of small–medium bees (*Megachilidae*) compared to the other sizes of bees were also reported (Cristofolini et al., 2012).

In most of the studies reviewed here only the visitors of the keel flowers are indicated; however, these visitors may easily include occasional visitors, nectar/pollen stealers, pollen/flower eaters among others (Shivanna, 2014). Similarly, it seems necessary to include both pollinator and floral sizes in any pollination study, because both flower and pollinators sizes may show differences from one area to another. This information (especially the size of the visitors) was not indicated in most of the studies.

Although they are not as extensive as in Fabales (Westerkamp, 1997; Westerkamp & Weber, 1997), the information on the keel flowers of non-Fabales angiosperm orders is very limited. For instance, while tripping mechanisms are reported for the keel flowers of Papilionoideae and Polygalaceae (Westerkamp & Weber, 1997), for other keel-flowered lineages among angiosperms the situation is unknown. Therefore, a broader study which covers all these lineages would provide a clearer answer for the evolution of keel flowers within angiosperms. Pollination studies on other angiosperm families with keel flowers may shed light on the results of the current survey. Similarly, choice tests of keel flower pollinators may reveal whether these pollinators actually move freely between different angiosperm keel flowers or not.

As a general conclusion, in contrast to literature which suggests that keel flowers are pollinated particularly by skilled and strong bees, this review shows that keel flowers are mainly pollinated by small to large long-tongued bees, from Apidae and Megachilidae families. In terms of size, keel flowers of Polygalaceae and other angiosperm lineages, and exemplar non-keeled Fabales flowers were not very different from Papilonoideae pollinators. However, the current study also highlights the lack of information in many pollination studies such as most effective pollinators and pollinator/floral sizes.

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