

REVIEW ARTICLE

Rewardlessness in orchids: how frequent and how rewardless?M. Shrestha^{1,2,3} , A. G. Dyer² , A. Dorin³ , Z.-X. Ren⁴  & M. Burd¹ 

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ABSTRACT

About one-third of orchid species are thought to offer no floral reward and therefore attract pollinators through deception. Statements of this idea are common in the botanical literature, but the empirical basis of the estimate is rarely mentioned. We traced citation pathways for the one-third estimate in a sample of the literature and found that the paths lead to empirical foundations that are surprisingly narrow. Moreover, recent measurements have detected minute quantities of sugar available to insect visitors in some orchids thought to be rewardless, raising the possibility of a pollination strategy that is largely deceitful but different to absolute rewardlessness. The orchids are a well-studied group and there is no doubt that rewardlessness is common in the family. However, greater empirical effort is needed to verify rewardlessness in orchids and to explore geographic and environmental variation in the proportion of rewardless species.

INTRODUCTION

Animal-pollinated species with rewardless flowers occur throughout the angiosperms, but such deceptive pollination is thought to be especially prominent among orchids (Dressler 1981; Dafni 1984; Dafni & Bernhardt 1990; Renner 2006). It is often noted that about one-third of orchid species offer no reward, an idea that has become entrenched among natural history generalizations (Table 1). The frequency of rewardlessness is sometimes described in qualitative ways, such as 'most common' in the *Orchidaceae* (Gaskett 2011) or as dominant within the family (Ren *et al.* 2011), yet it is surprising how often the stated value is one-third. The frequency of rewardlessness in the *Orchidaceae* (and how it compares to other families) is important because it provides a window into fundamental issues of pollination biology (Dafni 1984) and may have been a contributor to the diversification of the family (Cozzolino & Widmer 2005; Givnish *et al.* 2015). Thus, it is worth asking where this approximation comes from.

Estimating the frequency of rewardlessness among orchids is complicated by the variety of rewards and types of rewardlessness present in the family. In addition to nectar, rewards of pollen and pseudopollen, oils, resins and volatile fragrances are offered by various species (van der Pijl & Dodson 1966; Tremblay *et al.* 2005). Rewardless orchids may mimic the nectar-producing flowers of particular co-occurring plants, mimic aphids to entice predatory aphidophagous insects to flowers, mimic female insects to attract male pollinators by sexual deceit, or use non-specific floral signals to deceive visitors (Ivri & Dafni 1977; Dafni 1984; Dafni & Bernhardt 1990; Peakall &

Beattie 1996; Pemberton 2010; Jin *et al.* 2014). To complicate matters further, there are instances of combined reward and deception in which single flowers reward certain species of floral visitor while deceiving others (Dafni & Bernhardt 1990), or reward nectar-feeding males while deceiving ovipositing females (Stökl *et al.* 2011; Jin *et al.* 2014).

The phylogenetic distribution of rewards and deceit is also complicated. The early diverging Apostasioideae offer pollen as a reward (Kocyan & Endress 2001; Kocyan *et al.* 2004), while species in the Vanilloideae and Cypripedioideae appear to be nonrewarding (Neiland & Wilcock 1998; Cozzolino & Widmer 2005). The highly derived subfamilies Orchidoideae and Epidendroideae contain both rewarding and nonrewarding species (Givnish *et al.* 2015). Evolutionary transitions between nectarlessness and nectar production appear to have been quite labile even within tribes and genera (Inda *et al.* 2012; Johnson *et al.* 2013; Weston *et al.* 2014).

It can be difficult, amidst this variety, to assess rewards or deceit in particular taxa. The behaviour at epidendroid orchids of male euglossine bees, now known to collect volatile chemical rewards (terpenes and terpenoids) from the flowers, was misinterpreted for nearly a century (Roubik 2014). Observation of only males among pollinating insects of some *Diuris* species in Australia was taken as evidence of sexual deceit within the genus, but the sex ratio of visitors to *Diuris maculata* varies geographically, and *Diuris sulphurea* has been found to produce nectar, throwing doubt on the interpretation of deceit (Weston *et al.* 2014). The neotropical orchids *Trichosalpinx blaisdellii* and *T. reflexa*, thought to use deceptive pollination, have only recently been found to possess labellar papillae that contain

Table 1. Literature concerning the extent of rewardlessness in the *Orchidaceae*.

Source	Description and citations (where present)
Luo <i>et al.</i> (2019: 1)	...one-third of Orchidaceae have been shown not to provide a reward. . . . No-reward pollination mechanisms have been recorded in at least 32 angiosperm families, including 7,500 species, 6,500 of which belong to Orchidaceae (Jersáková <i>et al.</i> , 2006).
Fantinato <i>et al.</i> (2017: 952)	Orchids pollination is even more controversial because about 30% (Ackerman 1986) employ among the most complex deception systems known in angiosperms to secure pollination without offering rewards (Tremblay <i>et al.</i> 2005; Jersakova <i>et al.</i> 2006)... in non-rewarding orchids, food-deception is reported as the most common pollination mechanism (reported in 38 genera; Jersakova <i>et al.</i> 2006).
Henneresse <i>et al.</i> (2017: 279)	Deceptive pollination...occurs in about 30% of orchids (Jersáková <i>et al.</i> 2006; Claessens & Kleynen 2011), one of the most diversified angiosperm families...
Sonkoly <i>et al.</i> (2016: 343)	Floral deception evolved independently in at least 32 angiosperm plant families (Renner 2006) and is especially common in orchids, where more than one-third of the species (>6500 species) is pollinated deceptively (Girord [sic] <i>et al.</i> 2002).
Gijbels <i>et al.</i> (2015: 154)	Whereas most species offer substantial nectar rewards to entice pollinators (further referred to as 'rewarding orchids'), one third of the species mimics odours and visual stimuli to deceive pollinators with the promise of food or reproduction (further referred to as 'deceptive orchids') (Cozzolino & Widmer 2005).
Givnish <i>et al.</i> (2015: 8)	Deceit pollination characterizes one-third of all orchids [9,39].
Johnson <i>et al.</i> (2013: 1)	[9 Cozzolino S, Widmer A. 2005; 39 Jersáková J, Johnson SD. [sic] 2006] ... floral deception is now known to occur in at least 30–40% of the ca 27 000 species in the orchid family [3].
Papadopulos <i>et al.</i> (2013: 2)	[3. Jersáková J, Johnson SD, Kindlmann P. 2006] Approximately 8000–10 000 of these species [orchids] offer no floral reward, yet they rely on animal pollination [18,19].
Inda <i>et al.</i> (2012: 72)	[18. Scopece G, Cozzolino S, Johnson SD, Schiestl FP. 2010 19. Ackerman JD. 1986] ...deception is widespread in orchids...around one-third of orchid species use this strategy (e.g. Cozzolino & Widmer, 2005; Smithson, 2009).
Pansarin <i>et al.</i> (2012: 850)	About one third of the Orchidaceae, among others also species of <i>Pogonia</i> , <i>Isotria</i> and <i>Cleistesiposis</i> (as <i>Cleistes</i>), is believed to attract pollinators by deceit (van der Pijl & Dodson, 1966; Dafni, 1984; Ackerman, 1986; Dressler, 1993).
Jin <i>et al.</i> (2014: 2)	It is estimated that approximately one-third of orchids, approximately 6500 species, are pollinated through deception [8–12].
Claessens & Kleynen (2011: 218)	[Renner, 2006; Dafni, 1984; Cozzolino & Widmer 2005; Schiestl, 2005; Ren <i>et al.</i> 2011] Deceit is not limited to the genus <i>Orchis</i> but is a widespread phenomenon, occurring in about one-third of all orchids (van der Pijl & Dodson 1966; Ackerman 1986).
Meekers & Honnay (2011: 1792)	Approximately 8,000–10,000 orchid species (1/3 of the family) do not produce any nectar as they attract pollinators by deceit (Peakall & Beattie 1996; Renner 2005 [sic; correct citation is Renner 2006]; Smithson 2006).
CaraDonna & Ackermann (2010: 249)	Comprising 1/15 of all flowering plants, orchids may be the largest family of flowering plants with over 28,000 accepted species (Govaerts <i>et al.</i> 2010), at least 1/3 of which are food deceptive (van der Pijl & Dodson 1966).
Pemberton (2010: 276)	Because about one third of the orchids, or about 10,000 species, have no floral nectar (Neiland & Wilcock, 1998; Jersáková <i>et al.</i> , 2006; Vereecken, 2009; Jersáková <i>et al.</i> , 2009), the numerous pollinators of these plants must acquire the needed nectar from other plants.
Scopece <i>et al.</i> (2010: 98)	... about one-third of all orchid species (~ 6,500–10,000; according to Ackerman 1986) are nonrewarding. . .
Brodmann <i>et al.</i> (2009: 1368)	Approximately one-third of the world's estimated 30,000 orchid species are deceptive and do not reward their pollinators with nectar or pollen [1].
Case & Bradford (2009: 1)	[1. Nilsson (1992)] Particularly intriguing is the fact that nearly one-third of orchid species offer no apparent reward to their pollinators, instead tricking them into pollination by offering a bogus reward, such as food or sex (Schiestl, 2005).
Jersáková <i>et al.</i> (2009: 224)	The Orchidaceae has by far the greatest concentration of nonrewarding species. Approximately 6,000 species (one-third of the family) in 47 genera are estimated to be food deceptive (van der Pijl & Dodson 1966; Ackerman 1986; Renner 2005 [sic; correct citation is Renner 2006]; Jersáková <i>et al.</i> , 2006)
Smithson (2009: 152)	Today, many experimentally-validated examples of cheating of pollinators by plants are now known (Renner, 2005 [sic; correct citation is Renner 2006]), especially in the Orchidaceae where this strategy is surprisingly frequent (approximately one-third of described species; van der Pijl & Dodson, 1966; Renner, 2005 [sic; correct citation is Renner 2006]).
Vereecken (2009: 203)	This is particularly true in the Orchidaceae, where approximately one-third of all orchid species (i.e., ca. 10,000 species worldwide) achieve insect-mediated cross-pollination without providing a floral reward of any kind to their pollen vectors (Dafni 1984, 1987; Ackerman 1986; Nilsson 1992; Schiestl 2005; Jersáková <i>et al.</i> 2006).
Vereecken & Schiestl (2009: 1077)	Such cases of 'deceptive' pollination have evolved multiple times within the angiosperms (Renner, 2006) and they are particularly well represented in the orchid family, where approximately one-third of all 30 000 species known to science bear only rewardless flowers (Dafni, 1984; Nilsson, 1992; Cozzolino & Widmer, 2005; Schiestl, 2005; Tremblay <i>et al.</i> , 2005; Jersáková <i>et al.</i> , 2006, 2009).
Juillet <i>et al.</i> (2007: 147)	About one third of all orchid species are deceptive, i.e., not providing any reward to their pollinator.
Peakall (2007: 2483)	Food-deceptive pollination is estimated to occur in approximately one-third of all orchids.

(continued)

Table 1. (Continued)

Source	Description and citations (where present)
Salzmann <i>et al.</i> (2007: 720)	One third of the Orchidaceae, around 6500 species, are considered to be deceptive (Ackerman, 1986; Nilsson, 1992) and do not provide any form of reward to their pollinators.
Jersáková <i>et al.</i> (2006: 220)	...non-rewarding flowers are actually rather widespread among Orchidaceae — between 6500 and 9000 species (approximately one-third of the total) are believed to deceive insect pollinators (van der Pijl & Dodson, 1966; Dressler, 1981; Ackerman, 1986; Renner, 2005 [<i>sic</i>]).
Kindlmann & Jersáková (2006: 47)	This hypothesis may explain why almost one third of orchid species (8,000–10,000 out of the approximate 25,000 existing orchid species; DRESSLER 1990) are deceptive.
Renner (2006: 130–131)	Ackerman (1986) estimated that one-third of the Orchidaceae—that is, between 6500 and 10,000 species—are deceptive in some way, and Dressler (1993, 223) suggested that there are 4800 deceptive generalized “food flower” mimics (flowers that pretend to offer pollen or nectar but do not resemble a specific model) among the orchids.
Smithson (2006: 419)	Nectar production is absent in around one-third of orchid species (van der Pijl & Dodson, 1966; Gill, 1989), and occasionally in other plants.
Cozzolino & Widmer (2005: 487)	...one-third of orchid species are estimated to be food deceptive, and another presumed 400 species are sexually receptive (i.e. attracting pollinators by mimicking the mating signals of the female) [7], suggesting that pollination by deceit in orchids is an evolutionarily highly successful strategy. [7 Dafni, A. and Bernhardt, P. (1990)]
Schiestl (2005: 255)	...food deception...is especially frequent in orchids with about one third of the family, approximately 10,000 species, being food deceptive (Dafni 1984; Ackerman 1986; Nilsson 1992).
Tremblay <i>et al.</i> (2005: 3)	Although most orchids offer some type of reward, an unusually high number of species offer no reward whatsoever. About a third of all Orchidaceae are deceptive (van der Pijl & Dodson, 1966; Ackerman 1986; Nilsson, 1992).
Gigord <i>et al.</i> , 2002: 1389)	More than one-third of orchid species do not provide their pollinators with either pollen or nectar rewards.
Neiland & Wilcock 1998: 1660)	It has been estimated, however, that one-third of the [orchid] family are deceptive and that their pollinators receive no rewards at all (van der Pijl & Dodson, 1966; Ackerman, 1984 [<i>sic</i>]).
Peakall & Beattie (1996: 2207)	Most notable are those that employ deceit rather than food rewards to attract pollinators (Dafni 1984; Dafni 1986; Ackerman 1986). It is estimated that 10,000 orchid species (approximately one-third of the family) are pollinated in this way (Ackerman 1986).
Dressler (1993: 222–223)	...generalized food flower mimics may make up as much as a quarter of the orchid family. Gill (1990) [<i>sic</i> ; correct citation is Gill (1989)] suggests a third of the family, citing van der Pijl & Dodson (1966), but their calculation refers to orchids without nectar, including other systems, such as male euglossine pollination and specific mimicry.
Nilsson (1992: 255)	Most orchids provide a pollinator reward (e.g. nectar) like other angiosperms, but 8000–10 000 species act by deceit, i.e. are frauds that provide no reward [3]. [3 van der Pijl, L. and Dodson, C.H. (1966)]
Gill (1989: 467)	...there are many species of orchids that offer no nectar rewards to pollinators. Porsch (1909) [<i>sic</i> ; correct citation is Porsch (1908)] counted at least 1000 species of orchids that offer no nectar rewards; van der Pijl & Dodson (1966) estimate that probably 8000, or about one-third of all orchid species, are fundamentally deceptive!
Ackerman (1986: 108)	Flowers of a third or more of the Orchidaceae, perhaps 10,000 species, deceive their pollinators by some means or another (van der Pijl & Dodson, 1966; Ackerman 1985).

carbohydrates, lipids and proteins that are extracted by pollinating midges that normally suck haemolymph from insect prey (Bogarín *et al.* 2018).

A certain amount of detailed observation is required to confirm the absence of nectar (*e.g.* Hobbhahn *et al.* 2013). Techniques for detecting highly viscous nectar or minute quantities of food reward are especially elaborate (Power *et al.* 2018; Lindqvist *et al.* 2018; Shrestha *et al.* 2019). Nonetheless, nectar has been assessed mostly by visual inspection for liquid exudates in flowers, and even these records probably underestimate the extent of nectar secretion (Weston *et al.* 2014). Some Australian diurid orchids, long considered nectarless, secrete minute quantities of reward that attract floral visitors. Small but detectable quantities of sugar, mostly sucrose, are secreted at the base of the labellum or column of *Caladenia rigida* (Faast *et al.* 2009), *C. colorata* (Reiter *et al.* 2018), *C. versicolor* (Reiter *et al.* 2019a), *C. arenaria* and *C. concolor* (Reiter *et al.* 2019b), and *C. nobilis* (Phillips *et al.* 2020). In each case, the reward is sufficient to elicit feeding behaviours from insect visitors.

Given the difficulties of assessing rewardlessness, it is unsurprising that its frequency among orchids is known only roughly. Nonetheless, the inherent importance of such estimates for understanding plant–pollinator interactions and our own interest in the floral signals of orchids (Ren *et al.* 2011; Shrestha *et al.* 2019) led us to investigate the history of the commonly stated idea that one-third of orchids are deceitful. The foundations of this claim turn out to be surprisingly narrow. This is not to say that the one-third estimate is certainly incorrect or that current evidence would provide strong support for any other value. Our aim was to investigate the foundations of the widespread one-third claim in order to reopen the issue.

In order to do this, we searched the online database Biological Abstracts (Ovid) in October 2019 for works containing the words ‘orchid’, ‘pollination’ and any of ‘deceit’, ‘deception’ or ‘deceptive’, and obtained 263 hits. We read the abstracts to separate those articles concerned primarily with particular instances of deceptive pollination from those likely to include general statements about the frequency of deceptive

pollination, and then read the latter articles to locate specific claims. In addition, we repeated the search using the terms ‘orchid’ and ‘one-third’, and obtained 12 relevant hits. Finally, we added a few instances of published literature that we knew made the one-third claim, based on our familiarity with the scientific literature on orchids. We read these works, noting any statements of the frequency of rewardlessness, nectarlessness or deceit and the supporting citations. We then read the supporting works, noting in turn their supporting citations, and continued in this manner until the pathways led to independently derived empirical evidence. In total, we located 39 works that asserted some quantitative value of this frequency. We then diagrammed the chain of citations in order to visualize the citation pathways.

Nearly every mention of the frequency of rewardlessness, nectarlessness or deceit among orchids occurred in the Introduction of the articles we read, often in the opening paragraph, and the frequency was nearly always given as one-third (Table 1). In a few instances, these statements were made with no supporting citations, an indication that the idea of rewardlessness in one-third of the *Orchidaceae* has been sufficiently prevalent and accepted that it is not always thought necessary to provide specific support. Statements about the prevalence of deceit pollination were usually presented as a background for some argument about orchid reproductive ecology or evolution that does not depend on a precise estimate of its frequency. Thus, these statements were meant to create context, so that ‘one-third’ might be interpreted to mean something like ‘common although perhaps not a majority.’

The literature in Table 1 forms a dense network of citation pathways (Fig. 1) leading ultimately to three kinds of empirical support:

One set of pathways leads to reviews of deceit pollination in particular genera (Dressler 1981; Dafni 1984, 1987) or to a survey of reproductive ecology in temperate Australian and Mediterranean orchid floras (Dafni & Bernhardt 1990). These sources present numerous instances of rewardlessness, but they do not specifically estimate the overall frequency of nectarlessness or rewardlessness in the orchid family.

A second set of pathways lead eventually to an influential book by van der Pijl & Dodson (1966) that explicitly addressed the frequency of nectarlessness as follows: ‘Porsch (1908) estimated that 1,000 species of orchids have little or no nectar. We would extend that estimate to at least one-third of the known orchids, perhaps as many as 8,000 species’ (van der Pijl & Dodson 1966: 22). The estimate of van der Pijl & Dodson is, therefore, grounded in much older evidence from which they extrapolate. The basis of their extrapolation is not specified, but the implication is that it is a direct application of Porsch’s (1908) estimate to a contemporary understanding of species richness in the *Orchidaceae*.

What, then, was the nature of Porsch’s evidence? He was reviewing the occurrence of rewards other than nectar, such as food hairs, and noted the frequency of such alternative attractants among several tropical orchid genera: ‘If we overview the mentioned alternative rewards with regards to their distribution, considering the consistent flower morphology of the species-rich genera (*Maxillaria*, *Oncidium*, *Stanophea*), we can currently confidently say that, making modest assumptions, far more than 1000 orchid species use these biologically alternative reward tissues in the absence of nectar’ (Porsch 1908: 369, translation by T. Bochynek). That is, Porsch was making a claim specifically about nectarlessness but not rewardlessness – indeed, the claim was about the frequency of ‘alternative’ rewards.

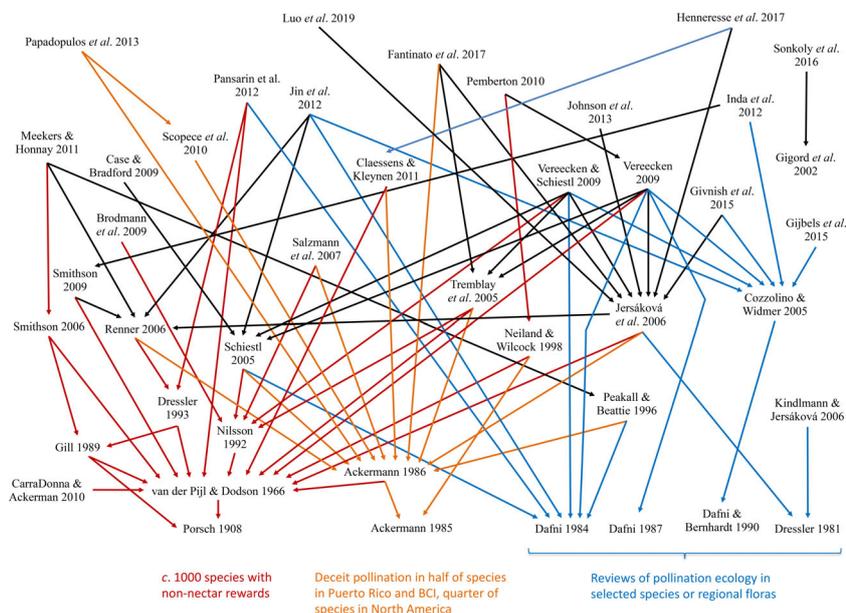


Fig 1. Citation paths for statements in Table 1 of the frequency of rewardlessness among orchid species. Arrows originate citing publications and point to cited publications. Paths coloured blue lead ultimately to articles that present surveys of reproductive ecology in regional floras (Dafni & Bernhardt 1990) or selected taxa (Dressler 1981; Dafni 1984, 1987; Claessens & Kleynen 2011). Paths in red lead to Porsch (1908); those in orange to Ackerman (1985). For the sake of visual clarity, a few arrows are omitted and pathways to and from Jersáková *et al.* (2009) are not shown; including them does not add new sources as final destinations of the pathways.

Finally, a third set of citation paths leads to a survey by Ackerman (1985) of orchid pollination in the floras of North America, Puerto Rico and Barro Colorado Island in Panama (Fig. 1). He categorized 337 orchid species as either autogamous, rewarding or deceptive. Roughly half the species in the two tropical floras, Puerto Rico and Barro Colorado Island, were deceptive, and about a quarter in the continental North American flora. The method for this estimate is more explicit than that of Porsch (1908), but Ackerman (1985: 100) warns, 'The basis for placing a species in one category or the other comes from the literature and personal experience, but at our present level of knowledge, much of this is admittedly guesswork.'

REASSESSMENT OF THE LITERATURE ON REWARDLESSNESS

Pollination biologists will be aware of the intensive studies of various mechanisms of deceit pollination in many orchid taxa, and the number of works identified in our Biological Abstracts search leaves no doubt that the phenomenon is widespread. However, it also seems clear that there are few original estimates of *how* widespread, perhaps only one (Fig. 1).

The idea that one-third of orchid species are rewardless seems to have originated with van der Pijl & Dodson (1966), who made a claim about species with 'little or no nectar.' They based their claim on an estimate by Porsch (1908) of the frequency of species with non-nectar rewards, but rewards nonetheless. Thus, the evidence of Porsch (1908) seems to have been erroneously generalized in citation to encompass both deception and nectarlessness. Ackerman's (1985) estimate of deceptive pollination in one-quarter of a temperate continental flora and one-half among tropical orchids might be taken as a rough corroboration of the one-third estimate, but one that raises the issue of geographic and ecological variation in the frequency of rewardlessness. Some additional evidence of this variation can be found in the descriptions of Claessens & Kleynen (2011) of 80 species (in 30 genera) of European orchids. Of these, 37 species (approximately 46%) are thought to be nonrewarding. Rewardlessness would appear, then, to be more prevalent in Europe than in North America, and closer to the frequencies in tropical floras, following Ackerman's (1985) estimates. Such geographic and environmental variation complicates any family-wide estimate.

Even within geographically circumscribed floras, caution over the prevalence of rewardlessness is needed because of uncertainty about the reward status of many orchids, as Ackerman (1985) noted regarding the species he considered. The case of ostensibly rewardless *Caladenia* orchids that actually produce minute rewards not visible or extractable as liquid nectar reinforces the need for caution about how rewardlessness has been determined in the past (Faast *et al.* 2009; Reiter *et al.* 2018, 2019a,b; Bogarín *et al.* 2018). Claessens & Kleynen (2011) highlight conflicting opinions from the literature and their personal observations about whether minute amounts of nectar are produced by species of *Himantoglossum*. They also note that small droplets can sometimes be observed on the labellum of *Malaxis monophyllos* and that insects inspect the labellum, but that it is not known if the droplets are nectar. It would certainly seem possible that there exist instances of

minute rewards in European orchids similar to the well-studied case of *Caladenia*.

Trace rewards may succeed as a pollination strategy by exploiting neural mechanisms in insect brains that code rewarding experiences. For example, the ventral unpaired median neuron (VUMmx1) of the honeybee (*Apis mellifera*) has been well characterized for associative learning mechanisms (Hammer 1993, 1997; Perry & Barron 2013). This neuron responds strongly for approximately 15 s even if only momentary sucrose stimulation is applied to the antennae with the touch of a sucrose-soaked toothpick (Hammer 1993). Some neural mechanism for detecting the quantity of rewards must also exist, since bees are known to prefer floral colours that had signalled higher reward volumes on a previous day (Gil & De Marco 2009). Nonetheless, a honeybee pollinator could experience a strong positive neural response from the mere presence of a reward, regardless of its quantity. Similarly, the small quantities of carbohydrates and proteins in papillae on the labellum of *Trichosalpinx blaisdellii* and *T. reflexa* flowers are thought to be 'flavour teases' that exploit the normal feeding behaviour of pollinating *Forcipomyia* midges (Bogarín *et al.* 2018). If neural mechanisms of reward detection can be exploited and are widespread among floral visitors, the use of such stingy rewards by orchids lacking visible nectar might also be widespread.

Pollinator manipulation by trace rewards might still be considered largely deceitful, but the nature of the deceit would be more complex and more subtle than in the case of complete absence of floral sugars. A paucity of reward may actually encourage appropriate flower-handling by visitors. For example, the rewardless orchid *Barlia robertiana* suffers substantially reduced pollinia export relative to controls when experimental nectar is added, apparently because visiting bumble bees respond to rewardlessness by probing flowers more vigorously (Smithson & Gigord 2001). A similar effect of tiny rewards in the hummingbird-pollinated orchid *Comparettia falcata* is described by Ackerman *et al.* (1994).

Differences among pollinators in their responses to stingy rewards might enhance the effective specificity an orchid species achieves even from a generalized pollinator guild (Fantinato *et al.* 2017). Pollinator responses to minute rewards may also influence movements among neighbouring plants and populations, thus affecting outcrossing rates and population differentiation (Cozzolino & Widmer 2005). Stingy rewards might diminish the negative frequency dependence of selection on Batesian mimics, commonly thought to be an important factor in orchid diversification (Jersáková *et al.* 2006). The hypothesis of a widespread stingy reward syndrome among orchids merits testing, especially as trace quantities of floral sugar are detectable in several orchid genera (Reiter *et al.*, b2018, 2019a; Shrestha *et al.* 2019; Phillips *et al.* 2020).

Repetition of the one-third claim has created a network of supporting citations in the literature (Fig. 1). Explicit citation is good practice in science, of course, yet abundant citation networks also pose risks if they tend to obscure where the empirical support for an idea lies. Repetition may create an illusion of certainty and consensus, or even propagate disproven or retracted arguments and evidence (Chen *et al.* 2013; van der Vet & Nijveen 2016; Letrud & Hernes 2019). Our point in this review is obviously not to insist that the one-third estimate is incorrect, but that it is unproven. Rather than accept a conventional figure,

we propose that the frequency of rewardlessness be considered an open question in need of empirical attention. We recommend that data be compiled on the phylogenetic, geographic and habitat distributions of rewardlessness and on types of rewardlessness, paying particular attention to the demonstrated and inferred occurrence of rewards, much in the manner of Table 5.4 in Weston *et al.* (2014). Such explicit compilations can be amended as new information on rewards becomes available. Even though one-third is recognized to be a very rough approximation, awareness of the narrow evidence underlying the one-third estimate can be a spur to precision in our knowledge of macroevolutionary patterns of rewardlessness and how deceit pollination has contributed to the diversification and biogeography of the orchids (Givnish *et al.* 2015).

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