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Promiscuous pollination of Australia's baobab, the boab, Adansonia gregorii

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Abstract. Australia's native baobab, *Adansonia gregorii* (F.Muell., Malvaceae: Bombacoideae) is the only baobab outside the African continent. Baobabs of the African continent have shades either of red, orange and yellow coloured flowers and are pollinated by insects, especially by hawkmoths of the Sphingidae family, or have white flowers and are pollinated by small mammals (e.g. bats and lemurs). In contrast, the Australian baobab, with white, erected flowers, was found to be mostly pollinated by hawkmoths. It is possible that for this white-flowered species, small mammals play a role in pollination. Therefore, the aim of the study was to identify major pollinators of the Australian baobab. Motion cameras were used in December 2013 and ground observations were performed in the flowering season of 2015–2016 to observe (potential) pollinators. Results show observations of hawkmoths and other insects, birds and sugar gliders (*Petaurus breviceps*) pollinating the flowers. The major pollinator found in this study was, however, the black flying fox (*Pteropus alecto*): it was observed foraging in groups and consuming the anthers of the Australian baobab flowers. Pollination by megabats, as the black flying fox, could have played an important role in the evolution of the white, erect flower of Australian baobabs.

Additional keywords: flower evolution, hawkmoths, Kimberley, megabats, P. alecto.

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Introduction

Pollination in baobabs present interesting case-histories, particularly as more details have become available about the evolution and biogeography of these iconic trees. There are nine species of baobab: two in mainland Africa (one recently discovered; Pettigrew *et al.* 2012), six in Madagascar, and one in Australia (Wickens 1982), the latter being the focus of the present study.

All baobab species have flowers that open at night (Baum 1995; Pettigrew *et al.* 2012). Four of the Malagasy species have flowers in shades of red, orange and yellow ('coloured'; Baum 1995; Pettigrew *et al.* 2012) that are mainly pollinated by hawkmoths (Baum 1995; Ryckewaert *et al.* 2011). All of the remaining baobab species in Africa have white flowers, which are probably visited mainly by small mammals (e.g. bats, bushbabies and lemurs; Baum 1995; Pettigrew *et al.* 2012).

The five species with white flowers show morphological differences with species with coloured flowers (Baum 1995; Pettigrew *et al.* 2012). The baobabs with white flowers have a staminal tube length between 8 and 50 mm, where the coloured flowers have much longer staminal tubes (between 60 and 190 mm; Baum 1995). The petals of the white flowers are smaller than those of the coloured flowers (8–15 and 12–24 mm, respectively, Baum 1995). Furthermore, the free

filaments of the coloured flowers, except the one of the Malagasy species, *Adansonia perreiri* Capuron, are larger than those of the white flowers (50–120 and 20–80 mm, respectively, Baum 1995). The baobabs with much more profuse and elongated spines, and with coloured flowers, are often insect-pollinated species (e.g. *Adansonia madagascariensis* Baill., Pettigrew *et al.* 2012).

Besides *A. madagascariensis*, all baobabs are regularly visited by hawkmoths (Baum 1995). Hawk moths hover in front of the flower while inserting the proboscis through the central filaments (Baum 1995). Due to the clean way of collecting the nectar, hawkmoths are often referred as 'nectar thieves' (e.g. Baum 1995). Bees and butterflies are often observed at baobabs in search of pollen and nectar; however, they do not contribute to the pollination due to infrequent visits and lack of contact with the stigmas (Baum 1995).

The mammals that take part in the pollination of some of the baobab species are larger in size than insects and can therefore transfer more pollen. Lemurs, for example, insert their snout into the flower and lick the nectar from the petal bases, which results in pollen on their face (Baum 1995). In *Adansonia suarezensis* H.Perrier and *Adansonia grandidieri* Baillon, small species of fruit bats were identified as major pollinator (Baum 1995). Unlike central-American, nectar-feeding phyllostomid microbats which can feed while hovering, African megabats first land on, or close to, the flower to lick nectar from the petal bases (Porsch 1935; Jaeger 1945; Baum 1995; Winter and von Helversen 1998).

One study shows that the Australian baobab, with white erected flowers, is pollinated by hawkmoths (Baum 1995). However, when comparing the morphology of the baobabs with white flowers (smaller staminal tubes, smaller petals and pollinated by mammals) to the baobabs with coloured flowers (pollinated mainly by hawkmoths and other insects; Baum 1995), it could be argued that the Australian baobab flowers are more similar to the mammal-pollinated flowers than to the hawkmoth-pollinated flowers. A similar conclusion can be drawn from the awkward positioning of the Australian baobab within the Longitubae, alongside four hawk moth pollinated baobab species with which it shares virtually none of the key features (see Table 1).

If, in fact, the boab proves to be mammal-pollinated, Baum's (1995) important generalisation will be consolidated, with a tight cluster of Madagascan baobabs that have unique features (e.g. the related attributes of hawk moth pollination, nocturnal coloured flowers and long staminal filaments), and the Australian baobab is placed in the mammal-pollinated group of baobabs, with white flowers like others in this group. A revised placement in the Brevitubae would then be consistent across many features, instead of in the Longitubae where this single species with white flowers would muddle Baum's (1995) strong generalisation provided by the four Madagascan, nocturnally coloured, hawk moth-pollinated baobab species with tightly-clustered features such as long stamina filamenst all absent from the Australian species.

Based on morphology of the flower of the Australian baobab, it seems likely that their main pollinators are mammals. However, this hypothesis has not yet been confirmed. Therefore, the aim of this study was to identify major pollinators and their interaction with the Australian baobab.

Materials and methods

Area

The data collection was performed in groves of Australian baobabs, *Adansonia gregorii* F.Muell, in the township of Kununurra, Western Australia, and near Oombulgari, Northern Territory in the monsoon season for 11 days in December 2013 and during a 12 day period between 23 December 2015 and

Table 1. Comparison of boababs in the Longitubae section (adapted from Baum 1995) Symbols used: present +: absent -: unknown ?

Species	Long staminal filaments	Coloured, nocturnal flowers	Hawkmoth pollination	Madagascar
Adansonia madagascariensis	+	+	+	+
Adansonia perrieri	+	+	+	+
Adansonia za	+	+	+	+
Adansonia rubrostipa	+	+	+	+
Adansonia gregorii (gibbosa)	-	-	?	-

5 January 2016. The data collection area has a wet–dry tropics climate, with an average ambient temperature during the data collection of 31.4°C, and average rainfall of 150.9 mm (Australian Bureau of Meteorology 2016). The flowering season of the Australian baobab is from late November through January, but can be flexible depending on the start of the wet season and peak number of flowers are 10–40 per tree per night (Baum 1995). Oombulgari is closer to the coast and was chosen to check for the possibility of visitations from small megabats known to visit mangroves (e.g. *Macroglossus minimus*, Gunnell *et al.* 1996).

Camera trapping

Four motion-sensitive cameras (UWay Night Xplorer NX 80HD, Wildlife Monitoring, Lugarno, NSW) were placed in different flowering baobabs around Kununurra for 10 days in a row and near Oombulgari for 2 days in a row. The cameras were set in baobabs, facing their flowers a couple hours before dark. The cameras were placed facing flowers where the corolla had pushed through the tip of the calyx. This could happen 12h before anthesis (Baum 1995). Cameras were active for 24 h and were moved daily to face different flowers. Every camera was placed in a different baobab, to minimalise the chance of multiple cameras capturing the same individual animal at the same time. Time-lapse photography (an option of the motion-sensitive cameras) was used during four observation nights to provide detail of the interaction between the pollinator and the flower. In addition to the motion-sensitive cameras, opportunistic data collection was performed with ground observations using a spotlight and single lens reflex plus flash camera (Canon EOS 700D, 70-300 mm lens) to further identify potential pollinator species.

Nocturnal survey

Eight nocturnal surveys were performed in the area of Kununurra, between 23 December 2015 and 5 January 2016. Each survey took ~90 min and was performed after dusk between 1900 and 2200 hours from a slow driving vehicle $(15-30 \text{ km h}^{-1})$. Surveys were conducted with a spotlight plugged into a Toyota V8 vehicle. When a flowering baobab tree was spotted, it was carefully investigated for potential pollinators for several minutes. Animals within a metre of a baobab flower were recorded as a potential pollinator, and when possible, photographed. On average 19 flowering baobabs were checked per survey.

Species identification

Photos were taken to identify the different pollinator species. Books were used for identification: 'A field guide to the mammals of Australia' by Knight and Menkhorst (2010), 'Australian birds: a concise photographic field guide' by Trounson and Trounson (2005), 'A guide to Australian moths' by Zborowski and Edwards (2007) and the 'Butterfly house, Sphingidae of Australia' by Herbison-Evans and Crossley (2014).

Kimberley hawkmoths are diverse: there are 18 known genera (Herbison-Evans and Crossley 2014). Hawkmoths genera were in most cases unidentifiable; however, size could be estimated based on the photos. Hawkmoths were categorised into two groups based on wingspan size in cm, 'large' wingspan between 12 and 13 cm and 'small' wingspan between 2.5 and 8.0 cm (Herbison-Evans and Crossley 2014).

Results

Pollination activity was observed at on average seven baobabs per survey. In total, 19 different animal species were recorded as potential pollinators of the Australian baobab.

Black flying foxes (Pteropus alecto)

During the transect walks in 2015–2016, between two and 12 black flying foxes (total n = 62) were observed per survey within a metre of an Australian baobab flower (Fig. 1). The black flying foxes were only observed in large trees, as these bats seemed to avoid smaller trees with delicate branches. Behavioural observations showed that flying foxes consumed the anthers of the *A. gregorii* flowers, as shown in Figs 2, 3. We did not observe flying foxes damaging the stigmas. The posture of feeding flying foxes appeared to be constrained by their large size and the difficulty of finding a strong-enough perch near the flower. For this reason it was common to observe them to hang vertically from a perch above the flower (Figs 2, 3).

Moths

On average five moths were recorded per survey (range 1-11; see Fig. 1). The number of recorded moths increased as the wet season progressed. Moths approached the flower from the side, outside the petals, 66.7% of time (Fig. 4b-d, g). In the minority of cases where the moth delivered its proboscis through the androecium, its length permitted a 'clean' interaction that did not involve pollen transfer from anthers to moth. In one case, a small moth appeared to 'crash land' on the anthers and pollen was transferred to the body. It proved difficult to make generic identifications

of hawkmoths from the camera images and transect walks. Five species of moths were observed, three from the 'large' wingspan group (n=23), of which *Agrius convolvuli* (Fig. 4*a*, *e*), and *Theretra oldenlandiae* (Fig. 4*f*) could be identified. Furthermore, two moth species of the 'small' wingspan group were observed (n = 14), one was potentially *Eudesmeola lawsoni*, and one could not be identified. The *Eudesmeola lawsoni* was observed landing on the bud of the flower and putting its proboscis outside the calyx to reach the nectar (Fig. 4*g*).

Moths were recorded only during the time lapse-setting of the trigger cameras, and not with the movement-sensitive setting. This is probably because the Passive infrared sensor in the cameras is primarily developed for detecting warm-blooded animals in motion, and does not work on small cold-blooded animals, such as insects (Steen and Thorsdatter Orvedal Aase 2011). Based on the transacts and time lapse photographs, we conclude that moths play a minor role in the pollination of the Australian boab tree.

Other insects

Three different bee species were observed: European bee (*Apis* mellifera; n=1), Carpenter bee (*Xylocopa virginica*; n=1) and the native bee (*Tetragonula* spp.; n=3). Furthermore, Leaf beetles (*Chrysomelidae* spp.; n=31) were observed consuming flowers of two baobabs, and a Potter wasp (*Abispa ephippium*, n=1) was spotted.

Sugar glider (Petaurus breviceps)

The motion-sensitive cameras captured indistinct images of sugar gliders (n=4; see Fig. 5). However, their presence (n=2) was confirmed during transect walks (Fig. 5). Behavioural observations showed that sugar gliders consumed both nectar and anthers.



Fig. 1. The absolute number of animals (with s.e.) recorded of the two most common pollinators, *Pteropus alecto* (grey) and hawkmoths (white) during transacts in the 12 day period in 2015–2016.



Fig. 2. (*a*) Multiple *Pteropus alecto* individuals hanging on substantial branches of *Adansonia gregorii*, searching for and visiting flowers. Note the choice of stout stems by this heavy megabat (\sim 800 g) and the adoption of a vertical hanging posture to improve secure access to the flower when a substantial purchase was unavailable next to the flower but was available above. (*b*, *c*) *P. alecto* hanging in a vertical posture, clearly grasping the flower to consume the anthers.

Birds

Seven different species of birds were recorded early morning: little friar bird (*Philemon citreogularis*; n = 1), silver-crowned friar bird (*Philemon argenticeps*; n = 1), blue-faced honeyeater (*Entomyzon cyanotis*; n = 2), white-gaped honeyeater (*Lichenostomus unicolor*; n = 3), black-chinned honeyeater (*Melithreptus gularis*; n = 2), great bowerbird (*Ptilonorhynchus nuchalis*; n = 1) and the brown honey eater (*Lichmera indistincta*; n = 4), of which one was observed roosting in a boab.

Discussion

The current study has identified both insect and mammals as pollinators for the Australian baobab. Studies on the pollination of baobabs, have had a chequered history. The earliest studies implicated small mammals as the most important pollinators (e.g. van der Pijl 1936; Wickens 1982), but later detailed work

in the Longitubae section of Madagascan baobabs (coloured nocturnal flowers, *viz*: *A. madagascariensis*, *A. perrieri*, *A. za*, *A. rubrostipa*) implicated hawkmoths as major pollinators (Baum 1995).

The same researcher (Baum 1995) concluded that hawkmoths are the main pollinator of the Australian boab, which shares no features with the other four species in the section, raising a question about its hawkmoth pollination. In answer to that question, the current study shows that *A. gregorii* is mammalpollinated, with the black flying fox (*P. alecto*) as the major pollinator.

Flower morphology

The flower morphology of the white-flowered *A. gregorii* has many similarities with the other mammal-pollinated baobab species. The staminal tubes from the *A. gregorii* flower as of the other white flowers are much smaller than those of the



Fig. 3. *Pteropus alecto* consuming the anthers of *Adansonia gregorii* flower. Note the pollen packets adhering to the muzzle and the vertical approach from a substantial stem.

coloured flowers from insect-pollinated boabs (staminal tube length: 8-50 vs 50-190 mm, respectively, Baum 1995). The free filament numbers of the white flowers is higher than the coloured flowers (150-1600 vs 90-250, respectively, Baum 1995). The peak number of flowers per night of the white flower baobabs is higher (10-50), than that of the coloured flowers (10-30; Baum 1995).

Flying foxes

Baum (1995) put the A. gregorii in the section Longitubae with insect-pollinated baobabs. The present study tends to return the emphasis to mammal pollination, by the black flying fox that was recorded 62 times near flowers of the Australian baobabs. The role of the flying fox in the pollination process was clearly dominant. First, since the flying fox was observed consuming the anthers, it could be considered a very effective pollinator, with both anthers and pollen particles observed on its snout. However, motion-cameras in this study revealed that the flying fox may not have been seeking the nectar (Figs 2, 3), even if this may have played a role in attracting this flying fox, just as nectar odour attracts megabats to the African baobab, A. digitata (e.g. van der Pijl 1936; Baum 1995). Second, P. alecto camps can contain between $500 \pm 10\,000$ animals, and even larger camps are common (Tidemann et al. 1999; Vardon and Tidemann 1999). P. alecto feed in groups and group sizes between 2 and 12 flying foxes were observed in the large trees, similar numbers were found in other large bat species (Heithaus et al. 1974). Third, compared with hawkmoths, flying foxes are bigger, can carry

bigger pollen loads, live longer, may be cognitively more sophisticated (Pettigrew *et al.* 1989; Fleming *et al.* 2009) and fly longer distances (50 km on a single nocturnal excursion; Hutson *et al.* 2008). Furthermore, pollination of the Australian baobab by flying foxes could be beneficial to *A. gregorii*. It may help conserve the genetic variety due to the long distances that bats travel (as is shown in African species; Djossa *et al.* 2015).

In contrast with our findings, Baum (1995) did not report any visits by bats to *A. gregorii*, although he did report a visit by *Rousettus* to *A. digitata*. The difference could be due to location of the observation sites. *P. alecto* camps are always located close to a creek, river or other water source (Hall and Richards 2000), as were our collection sites. The location of Baum's (1995) sites was unclear, but might have been further away from water.

Moths

In the current study at least five different moth species were recorded which was more than reported in literature (Baum 1995). Baum (1995) reported one species of hawkmoth, *Agrius convolvuli*, which was argued to be the main pollinator due to frequent contact with both stigma and anthers. In the current study *A. convolvuli* was also recorded; however, no contact with stigma or anthers was observed.

We suspect that the effectiveness of pollination by different hawkmoth species may vary. This was indicated by the method of nectar consumption; while the larger hawkmoths could consume nectar from a distance, using a long proboscis without making



Fig. 4. Hawkmoths in the vicinity of boab flowers, *Adansonia gregorii*: pollen transfer is largely non-existent or inefficient, except for the rare cases where the hawkmoth 'crash lands' on the anthers (not shown). (*a*) *Agrius convolvuli* extends its proboscis to the centre of the flower as it hovers. Most hawkmoth visits were 'clean' such as this one, with no transfer of pollen via the very long proboscis, which in this case extends to the middle of the androecium (seen more clearly in an enlarged image). (*b*) A small hawkmoth, attracted to the nectar sac at the flower's base. (*c*, *d*) Two different species of hawkmoths, where the target appears to be the perfumed nectar sac, as the proboscis is directed well outside of the anthers in both cases, clearly ineffective at pollen transfer. (*e*) *A. convolvuli* hovering close to the anthers. The only observed case where pollen was transferred after a closer encounter than this, was when a small hawkmoth 'crash landed' on the anthers (observed but not captured on camera). (*f*) Theretra oldenlandiae was spotted on a boab leaf within a metre of a boab flower. (*g*) *Eudesmeola* spp. observed landing on the bud of the flower and putting its proboscis outside the calyx to reach the nectar.

contact with the anthers (Fig. 4), the two smaller species tended to crash land on the androecium. The smaller species might therefore be more effective at transferring pollen. Furthermore, we observed the majority of moths approaching the flowers from the side without getting close to the anthers and without pollen transfer, which is in line with observations by Baum (1995).

More hawkmoths were observed at the end of the *A. gregorii* flower season. This observation is similar to that of Baum's

(1995) study, when fewer flowers were present compared with the beginning, when many flowers were observed. This makes the pollination of the *A. gregorii* by moths even less significant than previously indicated.

The results in the current study indicate that *A. convolvuli* is not the main pollinator of the *A. gregorii*, although it did visit the trees. In contrast, *A. convolvuli* has been identified as the main pollinator in over 70 grassland and savannah plant species in



Fig. 5. Sugar glider, *Petaurus breviceps*. Montages of single frames from a time lapse series of *P. breviceps* feeding on *Adansonia gregorii* flowers (white arrows point towards boab flowers; a-d). Telephoto and flash photograph of the species captured in a-d, the sugar glider (e).

Africa (Johnson and Raguso 2016). Including African species with white flowers with long tubes (~100 mm; Johnson and Raguso 2016), whilst the white flowers of the *A. gregorii* have relatively short tubes (25–50 mm; Baum 1995). This may explain why the hawkmoths are not the main pollinator in *A. gregorii*.

Other insects, birds and sugar gliders

The sugar glider is a known pollinator of other tree species (Goldingay *et al.* 1991), but was never reported as pollinator for *A. gregorii*. The sugar glider may also be an effective pollinator because it interacts strongly with the androecium of the flower and has been observed with large amounts of pollen adherent to its snout. Sugar gliders may probably pollinate within the tree or within a small group of trees. Its overall significance is most likely small, because of the low frequency of sugar gliders observed compared with the group size and abundance of the flying fox.

Honey eaters, bees and wasps were observed around dawn when most of the pollen had been consumed by flying foxes, so the early morning visitors would be unlikely to play a role in pollination. In addition, honey eaters were observed poking a hole at the base of the flower to get access to the nectar, and did not come in contact with present anthers. Leaf beetles (*Chrysomelidae*) were observed destroying and eating the entire flower, even when the flower was still closed. Thus, these are also not considered as significant pollinators of the Australian baobab.

Erected flower

Based on the results of this study we think that the large difference in the size of the black flying fox (~800 g mean weight; Markus and Hall 2004) may explain the divergent evolution of the Australian baobab pollination from its close relatives in Africa, which are pollinated by small megabats (*Epomophorus wahlbegii* (54–125 g) and *Rousettus aegyptiacus* (80–170 g; Porsch 1935; Jaeger 1945; Baum 1995).

The origin of the Australian baobab is obscure, but nITS gene sequence suggests that its closest relatives are two African baobab species with flowers on long pendant stalks (Vickers and Pettigrew 2015), which would be difficult to pollinate unless

the megabat involved was small. The contrasting erect flowers of the Australian species might be a response to the need of the black flying fox for a strong substrate to provide access for pollination as observed in Figs 2 and 3). Promiscuous pollination by vectors like birds, insects (particularly hawkmoths) and arboreal mammals may have played a vital role in the Australian baobabs arrival. However, the alleged loss of the long African stalk, along with the loss of the pendant habit and its inversion to give upright anthers could be explained by the constrained access of a heavy megabat such as *P. alecto*. Furthermore, the greater proximity of the stalk to a stout branch could also be explained if the evolution of the pollination syndrome were driven by a large megabat that needed to be able to land next to the flower before feeding.

Although this has not been investigated, the physical characteristics of the stout upright anthers may also have evolved to facilitate their consumption by *P. alecto*. The erect presentation of the *A. gregorii* flower is also consistent with our observations of both direct and hanging access from a supporting branch by the flying fox. Their weight (~800 g; Markus and Hall 2004) contrasts with the much smaller *Rousettus aegyptiacus* (145 g; Norberg 1972) and *Epomophorus wahlbergi* (90 g; Bergmans 1988), which are the major pollinators of the African baobab, *A. digitata* (Wickens 1982; Baum 1995). The erect presentation of anthers favours the black flying fox and contrasts with pendant flowers favouring smaller flying foxes. In addition, the *A. gregorii* has the greatest loss of pollen spines amongst all baobabs (Pettigrew *et al.* 2012), which is the opposite direction from what would be expected from insect pollination.

A. gregorii pollen is almost devoid of spines, which are also very short compared with other baobab pollen (Pettigrew *et al.* 2012). Insect-pollinated species have much more profuse and elongated spines (e.g. *A. madagascariensis*; Pettigrew *et al.* 2012). This suggests that the tendency to reduce spine number and size that has occurred with the mammal-pollinated, white-flowered baobabs has been taken even further in the *A. gregorri*. This is not what would be expected if insects were important pollinators. Thus, one can conclude that hawkmoths play only a minor role in pollination of *A. gregorri* compared with the black flying fox.

It is unclear why white flowers are mainly pollinated by mammals compared with the extraordinary visual optics of hawkmoths that can explain the coloured nocturnal flowers that are mainly pollinated by hawkmoths. These invertebrates have visual systems that do not suffer the scotopic limitations of vertebrates (Land and Nilsson 2015). Hawkmoths have superposition compound eyes (Warrant et al. 2003) that in effect use mirrors instead of lenses, resulting in a retinal image which is the brightest known in nature (Land and Nilsson 2015). As a result, they are able to discriminate colour at night (Land and Nilsson 2015). Furthermore, white flowers seem to stand out against vegetation and the night sky (Hopkins 1986). In contrast, many bat-pollinated flowers are dull in colour (Knudsen et al. 2006), which may function as camouflage from other visitors rather than a visual stimulus for bats (Knudsen et al. 2006). If this 'camouflage argument' has merit, it could also help explain the evolution of brightly coloured nocturnal flowers in hawk moth-pollinated baobabs, as these would have been detectable only by the hawk moths

themselves, because of their nocturnal colour vision provided by superposition optics.

Conclusion

From our study we conclude that the Australia's native baobab, *A. gregorii*, is dominantly mammal-pollinated by the black flying fox (*P. alecto*), instead of insect-pollinated as suggested in an earlier study. Three (potentially) identified, and two unidentified moth species were recorded as possible pollination vectors of the *A. gregorii*. Sugar gliders, birds, and other insects might also be partly responsible for pollination. The development of the upright flower posture of the Australian baobab might be an adaption to the pollination of the large size of the black flying foxes. With many morphological and pollinator similarities with the white flowered baobabs it might be necessary to reconsider the position of *A. gregorii* in the Longitubae section.

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