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Passerine Pollination of *Rhodoleia championii* (Hamamelidaceae) in Subtropical China

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ABSTRACT

The pollination ecology and breeding system of the Hamamelidaceae tree species *Rhodoleia championii* were studied in an evergreen broad-leaved forest in Nankunshan National Forest in Guangdong Province in China. *Rhodoleia championii* produces lipid-rich pollen grains and dilute nectar (averaging 0.7 mL/d and 9% sugar), with nectar production peaking before 0800 h; the species is self-incompatible and does not set seed asexually. Seven species of nectar-foraging birds visited the inflorescences, with the most common visitors being Japanese white-eyes (*Zosterops japonicus*, Zosteropidae) and fork-tailed sunbirds (*Aethopyga christinae*, Nectariniidae). Bumblebees and honeybees played limited roles as pollinators. As documented by fossils from Europe, the *Rhodoleia* stem lineage dates back at least to the Paleocene. Bird pollination, however, is unlikely to have evolved before the Oligocene when sunbirds arrived in Europe, and pollination by *Z. japonicus* cannot be much older than 250,000 million years ago, when *Z. japonicus* diverged from its closest relative.

Key words: *Aethopyga christinae*; bird pollination; European cretaceous fossils; Hamamelidaceae; nectar-feeding passerines; *Zosterops japonicus*.

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China is home to some 40 species of birds that forage for floral nectar (Mackinnon *et al.* 2000), but few of these bird/flower interactions have been studied (reviewed by Corlett 2004). Among Asian bird-pollinated species studied in some detail are *Bruguiera gymnorhiza* (Rhizophoraceae) and *Camellia japonica* (Theaceae). The former is a mangrove species that ranges from SE Asia through Micronesia and Polynesia to East Africa. In Thailand, it flowers in December/January and is an important nectar source for species of *Zosterops* (white-eyes) (Kondo *et al.* 1991). *Camellia japonica* occurs in China and Japan and flowers from the end of November to March/April; it, too, is pollinated by white-eyes (Yomoto 1988, Kunitake *et al.* 2004). The Chinese nectar-foraging birds belong to the Nectariniidae, Dicaeidae, Zosteropidae, Chloropseidae (synonym: Irenidae), and Pynonotidae (Mackinnon *et al.* 2000, Corlett 2004), with some species foraging mainly on introduced *Bombax*, *Erythrina*, *Calliandra* and *Callistemon* (Corlett 2004, 2005; http://www.wwfchina.org/birdgallery 2004-onwards; G. Lei, pers. obs. in Guangdong).

Here we contribute to the knowledge of Asian bird-pollinated species with a study of the pollination ecology of *Rhodoleia championii* Hook. f., a member of the Hamamelidaceae. *Rhodoleia championii* is a tree of evergreen broad-leaved forests occurring at an altitudinal range of 700–1000 m in Guangdong Province and the neighboring provinces Hong Kong, Guizhou, and Hainan (Yang *et al.* 1983). The genus *Rhodoleia* comprises about 10 species that occur in China, Vietnam, Thailand, Myanmar, Malaysia, Sumatra, and Indonesia (Exell 1933, Suddee & Middleton 2003, Zhang *et al.* 2003). There are six species in China of which three are endemic (Yang *et al.* 1983). *Rhodoleia* is most closely related to *Exbucklandia*, which comprises four species distributed from the Himalayas to Burma, Indo-China, southern China, Peninsular Malaysia, and Sumatra (Magallón 2007). Together, *Rhodoleia* and *Exbucklandia* form the sister clade to the other 25 genera of Hamamelidaceae (Li *et al.* 1999, Stevens 2001-onwards, Magallón 2007). Unlike most Hamamelidaceae, which have inconspicuous, usually unisexual flowers, *Rhodoleia* has bisexual flowers borne in tight heads, each with four to six flowers that are vividly pink to purplish, scentless, and nectar producing. Bird pollination in *Rhodoleia* was first documented in the Buitenzorg Botanical Garden, where Doctors van Leeuwen (1927) observed white-eyes, sunbirds (*Aethopyga*), spider-hunters (*Arachnothera*), and bulbuls (*Pycnonotus*) taking nectar from *Rhodoleia teysmanni*. Very rarely there were visits by *Bombus* and a few wasps. On Hong Kong Island, Corlett (2001) recorded *Zosterops japonica* and *Aethopyga christinae* on *R. championii*.

We here report on the floral phenology, nectar secretion pattern, pollinators, and breeding system of *R. championii* and then discuss the evolution of bird pollination in the Hamamelidaceae, a family whose pollination has rarely been studied (Anderson & Hill 2002: *Hamamelis*; Xiao *et al.* 2004: *Disanthus*). Hamamelidaceae have a rich fossil record that extends from the Upper Cretaceous to the Miocene (Mai 2001, Magallón 2007, Benedict *et al.* 2008), and fossil fruits and seeds of *Rhodoleia* have been described from the Upper Cretaceous (Maastrichtian) and Tertiary of Europe (Mai 1968, 2001; Knobloch & Mai 1986). This raises the question of how long this Laurasian lineage may have interacted with nectar-foraging birds.

METHODS

Study sites and species.—The study sites were located in the Nankunshan National Forest Park in Guangdong Province, China (23°38′ N, 114°38′ E, *ca* 700 m asl). *Rhodoleia championii* is a dominant species of the local evergreen broad-leaved forest; the density of *R. championii* trees in the areas is *ca* 450/ha (Yang *et al.*

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1983). Observations and pollination experiments were carried out between 28 December 2005 and 5 April 2006 at two sites in the park, located 5 km apart, one a natural patch of mixed forest with many individuals of *R. championii*, the other a stand of about 200 individuals of *R. championii* planted for horticultural use. At both study sites, air temperatures during the day were recorded about once every hour. We selected and marked 20 trees (30–40 cm dbh and 7–13 m in height) from among hundreds in bloom for the pollination experiments and 8 for pollinator observation.

NECTAR SECRETION.—Nectar production was measured once a day at 1200 h by extracting all nectar with 1 mL syringes (a fresh syringe each day) from all flowers in 20 inflorescences (on 12–14 January 2006). Between extractions, the inflorescences were bagged with fine nylon mesh. In addition, diurnal patterns of nectar secretion were monitored by sampling 20 bagged inflorescences at 2-h intervals over a period of 24 h. The sugar concentrations of the sampled nectar were estimated in terms of sucrose equivalents using a handheld refractometer.

POLLEN HISTOCHEMISTRY AND STIGMA RECEPTIVITY.—Pollen was collected from dehiscing anthers to examine its starch and lipid contents by staining the grains with iodine in aqueous potassium iodide (IKI) or Sudan IV solutions, before examination under a microscope. Stigma receptivity was tested just after flower opening and then every 2 h until the end of anthesis, using MTT (3-4,5-dimethylthiazol-2-yl-2,5-diphenyl-tetrazolium bromide, Sigma M-2128, Sigma, St. Louis, MO, USA) as described by Dafni (2001). In addition, pollen from dehiscing anthers was collected at 2-h intervals, tested with MTT; pollen grains were considered viable when they were fully stained, suggesting normally formed cytoplasm (Rodriguez-Riano & Dafni 2000).

POLLINATION EXPERIMENTS.—Between 12–14 January and 14–16 February, five treatments were applied to the flowers and inflorescences of 20 trees to examine the breeding system and the effectiveness of different visitors as pollinators: (1) *Open*—inflorescences exposed to visitors without any manipulation; (2) *Emasculated and hand cross-pollinated*—bagged flowers were emasculated before the anthers dehisced and then hand-pollinated with fresh pollen taken from the flowers of trees at least 100 m away; (3) *Untreated*—inflorescences were bagged before anthesis, but received no further manipulation; (4) *Hand self-pollinated*—inflorescences were bagged before anthesis and then hand-pollinated with pollen taken from dehiscing anthers on the same plant; (5) *Emasculated*—flowers were tested for agamospermy by emasculation of all the anthers before opening, followed by bagging and later checking for fruit set.

Fine nylon mesh was used for bagging, and pollen was transferred using Chinese calligraphy brushes in the hand-pollination treatments, using trees from outside the experimental area as pollen donors in the cross-pollination treatment. *Rhodoleia* pollen is rich in pollenkitt and sticky; it is not dispersed by the wind. Immature fruits were counted 30 d after the onset of the experiment, and mature fruits were counted a month later.

FLORAL VISITORS.—Visitors were observed through binoculars between 16 and 28 February 2006, including one full night of observation at the natural forest site, using an electric torch. Two days of diurnal and 6 h of nocturnal observations were also carried out in the planted stand during the same period. Visiting frequency was recorded as the number of inflorescences that a visitor interacted with on a single tree in 1 h. The numbers of visitors and of inflorescences on each visited tree were extrapolated from observations on single branches. A mist net was used to catch the birds visiting *R. championii* and photographs in bird guides were used to identify them. Bill length (upper mandible length) measurements were taken from white-eye and sunbird specimens in the Biological Museum of Sun Yat-Sen University to measure the potential for pollinator relationships between these birds and *Rhodoleia* flowers. The bird skins studied came mainly from Guangdong Province.

RESULTS

FLORAL CHARACTERS.—The inflorescence heads of *R. championii* are pendulous and comprise four to six flowers with pink to purplish-red petals and tan-pubescent bracts (Fig. 1A). The hypanthium and peduncle are sturdy (Fig. 1B, peduncles in fruit) and can withstand pecking by a bird's bill. There are four to six pairs of styles and 36–48 stamens per inflorescence. The styles are 29 ± 0.6 mm long (mean $\pm$ SE) and the filaments 30 ± 0.7 mm.

Flowering began in late December 2005 and ended in early March 2006. Single inflorescences lasted 5–7 d. Flowers opened before noon, without any perceptible odor. MTT staining showed that the stigmas were receptive just after flowers opening. Anthers began to dehisce 4–6 h after the onset of anthesis, and pollen was available for 2–4 d. Stigmas wilted shortly after most pollen had been dispersed, and this was followed by withering of the petals and filaments. Medium-sized trees produce about 2400 simultaneously blooming inflorescences.

NECTAR SECRETION PATTERN.—Nectar secretion began shortly after anthesis and peaked in the early morning, with dilute nectar so abundant that it collected among the filaments and ovaries at the bottom of the inflorescence cup (Fig. 1C). The amount of nectar produced per inflorescence per day was 0.7 mL ($N = 20$), with an average sugar concentration (in sucrose equivalents) of 9 percent ($N = 20$). Changes in nectar volume and concentration at 2-h intervals during the day are shown in Fig. 2. Little nectar was produced after 1400 h, until secretion began again the following day. Nectar sugar concentration was fairly constant throughout the day.

POLLEN HISTOCHEMISTRY AND POLLEN VIABILITY.—Pollen grains stained slightly with IKI solution and more strongly with Sudan IV. Under the microscope, Sudan IV-stained pollen showed conspicuous oil drops. Changes in pollen viability and stigma receptivity at 2-h intervals are shown in Fig. 3. Pollen viability declined

FIGURE 1. (A) Inflorescences of *Rhodoleia championii*; (B) Fruits of *R. championii*; (C) Nectar drops among filaments; (D) A *Zosterops japonicus* individual visiting an inflorescence; (E) An *Aethopyga christinae* individual visiting an inflorescence; and (F) Pollen grains on the forehead feathers of a *Zosterops japonicus*.

rapidly about 22 h after the anthers opened, while stigma receptivity remained constant.

FLORAL VISITORS.—Seven species of nectar-foraging birds visited the inflorescences (Table 1, which also shows species authors). The most common were Japanese white-eyes (*Zosterops japonicus*) and fork-tailed sunbirds (*Aethopyga christinae*; Fig. 1D and E). In the planted *Rhodoleia* stand, European honeybees (*Apis mellifera*, Apidae) collected pollen from *Rhodoleia* flowers, while in the 5 km

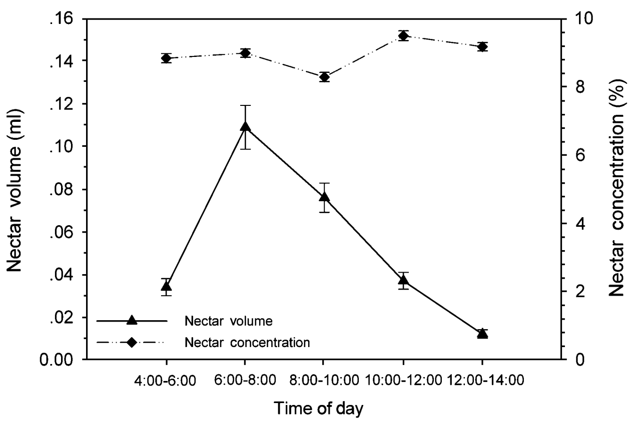

FIGURE 2. Changes in nectar volume and concentration ($\overline{X} \pm$ SE) of *Rhodoleia championii*.

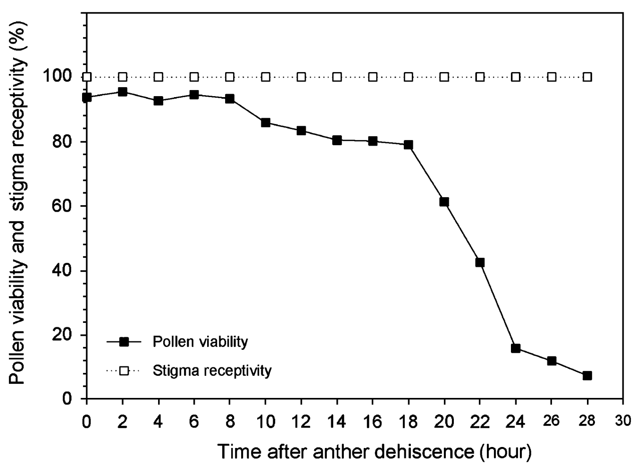

FIGURE 3. Changes in pollen viability and stigma receptivity of *Rhodoleia championii* during anthesis.

TABLE 1. *Visitors observed on* Rhodoleia championii. *Visiting frequency: ††† = very frequent, †† = frequent, † = rare. Reward: N = nectar, P = pollen.*

Floral visitor (FAMILY and species)	Visiting frequency	Reward
ZOSTEROPIDAE		
Zosterops japonicus Temminck and Schlegel, 1845	†††	N
Zosterops erythropleurus Swinhoe, 1863	††	N
NECTARINIIDAE		
Aethopyga christinae Swinhoe, 1869	†††	N
Aethopyga gouldiae Vigors, 1831	†	N
IRENIDAE		
Chloropsis hardwickii Jardine and Selby, 1830	††	N
PYCNONOTIDAE		
Pycnonotus jocosus L., 1758	†	N
Pycnonotus sinensis J. F. Gmelin, 1789	†	N
Hypsipetes mcclellandii Horsfield, 1840	††	N
Hypsipetes leucocephalus J. F. Gmelin, 1789	†	N
APIDAE		
Apis mellifera	††*	P
Bombus spp.	†	P

*Species only recorded at the planted stand.

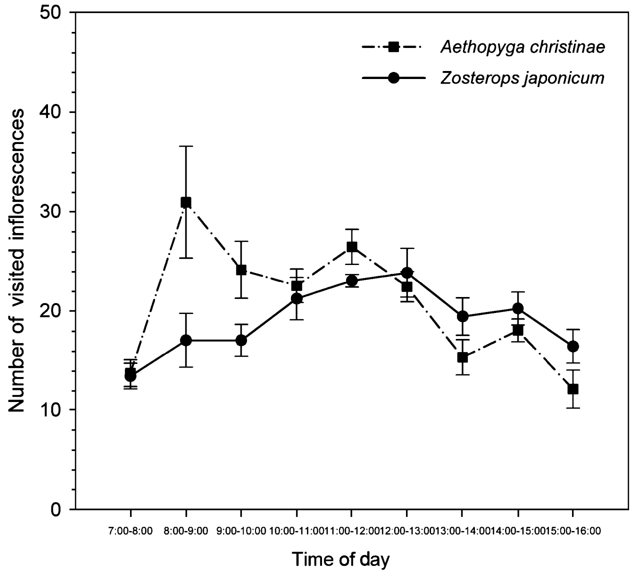

FIGURE 4. Visiting frequencies (times/h/tree) of white-eyes and sunbirds on *Rhodoleia championii* trees at Nankunshan National Forest in Guangdong Province in China.

distant natural forest, no honeybees were seen visiting the flowers despite the presence of beehives in the general area. Bumblebees (*Bombus* spp., Apidae) rarely visited *Rhodoleia* at either site. Temperatures at the forest site ranged from 9.2°C to 14.5°C; temperatures in the planted *Rhodoleia* stand rose to about 20°C at noon. During the nocturnal observations, no visitors were observed at either the planted or the natural sites.

White-eyes moved in flocks of 30–50 birds, while the sunbirds usually visited singly or in pairs. White-eye flocks swept the observation area five to six times an hour, usually from the same direction, while several pairs of sunbirds and leafbirds (*Chloropsis hardwickii*) stayed in the area foraging on one or two trees continually. Small birds were often driven away from inflorescences by bigger birds: Thus, white-eyes, the smallest birds visiting *R. championii*, were forced away by leafbirds. Nectar foraging on *Rhodoleia* started at about 0700 h and continued until about 1600 h, when activity declined; visiting frequencies of white-eyes and fork-tailed sunbirds during the day are shown in Fig. 4. White-eye feeding peaked around noon, that of sunbirds around 0900 h.

The bill lengths (means ± SE) of the white-eye and sunbird specimens measured in the Museum of Sun Yat-Sen University were as follows: *Z. japonicus*, 9.3 ± 0.2 mm (♂, $N = 21$) and 9.4 ± 0.2 mm (♀, $N = 15$); *A. christinae*, 13.4 ± 0.1 mm (♂, $N = 30$) and 13 ± 0.3 mm (♀, $N = 19$). Thus, bills were shorter than the filaments (30 ± 0.7 mm) and styles (29 ± 0.6 mm) of *R. championii*, forcing birds to insert their faces deeply into the flowers/inflorescences. A white-eye specimen caught in the mist net, had a great deal of pollen on the forehead and neck feathers (Fig. 1F).

POLLINATION EXPERIMENTS.—At 30 d after the experiment, no fruits had developed in emasculated or self-pollinated inflorescences, demonstrating that *R. championii* is self-incompatible and incapable of agamospermy. Initial fruit set in open-pollinated flowers was 63 percent (160 fruits of 254 flowers on 11 trees) and 82 percent in emasculated hand cross-pollinated flowers (83 fruits of 101 flowers on 17 trees), which is not significantly different ($G = 13.1$, df = 1, $P = 0.0003$). Fruit set in the same flowers monitored a month later, after numerous immature fruits had aborted, was 58 and 48 percent, respectively, values that are also not significantly different ($G = 3.1$, df = 1, $P = 0.08$). Clearly, however, the percentage of immature fruits aborting in the hand cross-pollinated inflorescences (42%) was higher than that in the open-pollinated inflorescences (8%; $G = 37.9$, df = 1, $P < 0.0001$).

DISCUSSION

BREEDING SYSTEM AND POLLINATION OF *RHODOLEIA*.—In its natural habitat, *R. championii* bears abundant flowers and fruits, and the results obtained here show that this is due to animal pollination since *Rhodoleia* is self-incompatible and likely incapable of agamospermy. Nine species from four passerine families were observed pollinating *R. championii*, while *Bombus* and *Apis* played negligible roles as pollinators. The major pollinators at Nankunshan were Japanese white-eyes (Table 1). When visiting the brush-shaped flower clusters, these birds always touched the anthers and stigmas, transferring pollen grains picked up during previous visits. Other plants in Guangdong Province and adjacent Hong Kong pollinated by white-eyes include species of *Camellia* as well as introduced horticultural species of *Bombax*, *Erythrina*, *Calliandra*, and *Callistemon* (Corlett 2004, 2005; G. Lei, pers. obs. in Guangdong). During the winter months in China (December to February), white-eyes congregate in large flocks (Mackinnon *et al.* 2000), and their visiting mode of sweeping an area tree-by-tree probably makes them efficient cross-pollinators. In contrast, leafbirds and sunbirds forage singly and usually remain on just one or two trees for long periods of time.

Seasonal food shortages can force birds that normally forage on fruits, seeds, and insects to use nectar as a supplementary energy source. For white-eyes this is well documented (Craig & Hulley 1996, Chen & Chou 1999, Symes *et al.* 2008). The relative shortage of fruits and seeds during the winter months at our study sites can be inferred from the fact that only 1.9 percent (8 of 412) of the woody plant species found on Hengshan Mountain, situated about 500 km north of Nankunshan, fruit between December and February (Peng *et al.* 2005).

In experimental situations, honeybees begin to visit flowers when temperatures exceed 15°C (Li *et al.* 2006). The highest temperature recorded at our forest study site was 14.5°C, while the temperatures in the planted *Rhodoleia* stand at noon rose to about 20°C, explaining why honeybees were frequently observed there, but not at the cooler forest site. The average highest daytime temperatures for December, January, and February recorded at Nankunshan from 1971 to 2000 are 13°C, 12°C, and 13.6°C (data from Guangdong Provincial Meteorological Bureau). These long-term temperatures and our own observations suggest that honeybees rarely pollinate *R. championii* in Nankunshan because the temperatures are too low. Bumblebees, on the other hand, were observed by Doctors van Leeuwen (1927) on *R. teysmanni* in Java and by us on *R. championii* in Nankunshan.

THE EVOLUTION OF BIRD POLLINATION IN HAMAMELIDACEAE.—Today, *Rhodoleia* occurs in China, Vietnam, Thailand, Myanmar, Malaysia, Sumatra, and Indonesia. However, seeds and fruits attributed to *Rhodoleia* have been described from the Upper Cretaceous (Upper Maastrichtian), Upper Paleocene, Upper Eocene, and Lower and Upper Miocene of eastern Germany (Mai 1968, 2001). Photos of these fossils match the seeds and fruits of extant *Rhodoleia* well. A study that used other Hamamelidaceae fossils as calibration points and two relaxed molecular clock approaches estimated the divergence of *Rhodoleia* from *Exbucklandia*, its sister group (see "Introduction") as dating back to 43 ($\pm$5) to 73 ($\pm$5) million years ago (Ma), depending on the clock approach used (Ickert-Bond & Wen 2005). Of the four species of *Exbucklandia*, one has bisexual flowers and three have unisexual flowers with extremely reduced petals, suggesting wind-pollination. The high age of the *Rhodoleia* stem lineage documented by fossils and inferred from molecular clocks raises the question of who pollinated *Rhodoleia* in the Early Tertiary or Upper Cretaceous. The oldest Passeriformes in Europe are from the Late Oligocene, those in Eastern Asian from the Miocene (Mayr & Manegold 2004; G. Mayr, Forschungsinstitut Senckenberg, Frankfurt, pers. comm., November 2008). Thus, *Rhodoleia* could have been pollinated by birds from the Oligocene onwards. The interaction between *Rhodoleia* and *Z. japonicus*, however, is extremely young. A dated molecular phylogeny for *Zosterops* inferred the divergence between *Z. japonicus* and its sister species, *Z. palpebrosus*, to be $<$ 250,000 Ma old (Moyle *et al.* 2009; R. Moyle, pers. comm.). This provides a striking example of the evolutionary plasticity of pollination interactions.

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LITERATURE CITED

ANDERSON, G. J., AND J. D. HILL. 2002. Many to flower, few to fruit: The reproductive biology of *Hamamelis virginiana* (Hamamelidaceae). Am. J. Bot. 89: 67–78.

BENEDICT, J. C., K. B. PIGG, AND M. L. DEVORE. 2008. *Hamawilsonia boglei* gen. et sp. nov. (Hamamelidaceae) from the late Paleocene Almont flora of central North Dakaota. Int. J. Plant Sci. 169: 687–700.

CHEN, C. C., AND L. S. CHOU. 1999. The diet of forest birds at fushan experimental forest. Taiwan J. For. Sci. 14: 275–287 (in Chinese with English abstract).

CORLETT, R. T. 2001. Pollination in a degraded tropical landscape: A Hong Kong case study. J. Trop. Ecol. 17: 155–161.

CORLETT, R. T. 2004. Flowering visitors and pollination in the oriental (Indomalayan) region. Biol. Rev. 79: 497–532.

CORLETT, R. T. 2005. Interactions between birds, fruit bats and exotic plants in urban Hong Kong, South China. Urban Ecosyst. 8: 275–283.

CRAIG, A. J. F. K., AND P. E. HULLEY. 1996. Supplementary head moult in cape white-eyes: A consequence of nectar feeding? J. Field Ornithol. 67: 358–359.

DAFNI, A. 2001. Field methods in pollination ecology. Course manual, second international pollination course. University of Haifa, Haifa, Israel.

DOCTORS VAN LEEUWEN, W.M. 1927. Vogelbloemen. 3. *Rhodoleia teysmanni* Miq. Trop. Natuur 16: 2–6.

EXELL, A. W. 1933. A revision of the genus *Rhodoleia*. Sunyatsenia 1: 95–102.

ICKERT-BOND, S. M., AND J. WEN. 2005. Phylogeny and biogeography of Altingiaceae: Evidence from combined analysis of five non-coding chloroplast regions. Mol. Phylogen. Evol. 39: 512–528.

KNOBLOCH, E., AND D. H. MAI. 1986. Monographie der Früchte und Samen in der Kreide von Mitteleuropa. Rozpravy Ustredniho Ustavu Geologického 47: 1–219.

KONDO, K., T. NAKAMULA, T. PIYAKARNCHANA, AND W. MECHVICHAI. 1991. Pollination in *Bruguiera gymnorhiza* (Rhizophoraceae) in Miyara River, Ishigaki Island, Japan, and Phangnga, Thailand. Plant Spec. Biol. 6: 105–110.

KUNITAKE, Y. K., M. HASEGAWA, T. MIYASHIMA, AND H. HIGUCHI. 2004. Roles of a seasonal specialist bird *Zosterops japonica* on pollen transfer and reproductive success of *Camellia japonica* in a temperate area. Plant Spec. Biol. 19: 197–201.

LI, J.-H., A. L. BOGLE, AND A. S. KLEIN. 1999. Phylogenetic relationships of the Hamamelidaceae inferred from sequences of internal transcribed spaces (ITS) of nuclear ribosome DNA. Am. J. Bot. 86: 1027–1037.

LI, J.-L., W.-J. PENG, J. WU, J.-D. AN, Z.-B. GUO, Y.-M. TONG, AND J.-X. HUANG. 2006. Strawberry pollination by *Bombus lucorum* and *Apis mellifera* in greenhouses. Acta Entomol. Sin. 49: 342–348 (in Chinese with English abstract).

MACKINNON, J., K. PHILLIPPS, AND F. Q. HE. 2000. A field guide to the birds of China. Oxford University Press, Oxford, UK.

MAGALLÓN, S. 2007. From fossils to molecules: Phylogeny and the core eudicot floral groundplan in Hamamelidoideae (Hamamelidaceae, Saxifragales). Syst. Bot. 32: 317–347.

MAI, D. H. 1968. Zwei ausgestorbene Gattungen im Tertiär Europas und ihre florengeschichtliche Bedeutung. Palaeontographica B 123: 189–199.

MAI, D. H. 2001. The fossils of *Rhodoleia* Champion (Hamamelidaceae) in Europe. Acta Palaeobot. 41: 161–175.

MAYR, G., AND A. MANEGOLD. 2004. The oldest European fossil sunbird from the early Oligocene of Germany. Naturwissenschaften 90: 173–177.

MOYLE, R. G., C. E. FILARDI, C. E. SMITH, AND J. DIAMOND. 2009. Explosive pleistocene diversification and hemispheric expansion of a "great speciator". Proc. Natl. Acad. Sci. USA 106: 1863–1868.

PENG, Z.-B., S.-P. FAN, AND J.-J. KUANG. 2005. Characteristics and domestication of the tree species in the Nanyue Arboretum. Hunan Science and Technology Press, Changsha, China.

RODRIGUEZ-RIANO, T., AND A. DAFNI. 2000. A new procedure to assess pollen viability. Sexual Plant Reprod. 12: 241–244.

STEVENS, P. F. 2001 onward . Angiosperm phylogeny website, version 9, June 2008. Available at http://www.mobot.org/MOBOT/research/APweb/ (accessed November 25, 2008).

SUDDEE, S., AND D. J. MIDDLETON. 2003. *Rhodoleia* (Hamamelidaceae), a new generic record for Thailand. Thai For. Bull. (Botany) 31: 132–135.

SYMES, C. T., S. W. NICOLSON, AND A. E. MCKECHNIE. 2008. Response of avian nectarivores to the flowering of *Aloe marlothii*: A nectar oasis during dry South African winters. J. Ornithol. 149: 13–22.

XIAO, Y.-A., P. HE, AND X. H. LI. 2004. Floral syndrome and breeding system of the endangered plant *Disanthus cercidifolius* Maxim. var. *longipes*. Acta Phytoecol. Sin. 28: 333–340 (in Chinese with English abstract).

YANG, Y.-Y., T.-S. TSENG, AND Y.-Q. XU. 1983. On the main forest-types and the structure characters of the communities in Nan Kun Mountain. J. South Chin. Agri. Univ. 4: 11–20 (in Chinese with English abstract).

YOMOTO, T. 1988. Pollination systems in the cool temperate mixed coniferous and broad-leaved forest zone of Yakushima Island. Ecol. Res. 3: 117–129.

ZHANG, Z.-Y., H.-T. CHANG, AND P. K. ENDRESS. 2003. Hamamelidaceae. *In* The Flora of China editorial committee (Eds.). Flora of China, Vol. 9, pp. 18–42. Science Press, Beijing, China.