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‘Good Heavens what insect can suck it’ – Charles Darwin, *Angraecum sesquipedale* and *Xanthopan morganii praedicta*

JOSEPH ARDITTI¹*, JOHN ELLIOTT², IAN J. KITCHING³ and LUTZ T. WASSERTHAL⁴

¹Department of Developmental and Cell Biology, University of California, Irvine, CA 92697, USA

²Department of Psychology, National University of Singapore, S117570, Singapore

³Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

⁴Department of Biology, University of Erlangen, Staudtstrasse 5, 91058 Erlangen, Germany

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In this review we provide a detailed description of Darwin’s prediction of the coevolution of a long-spurred orchid, *Angraecum sesquipedale*, and a long-tongued moth, his correspondence on the subject, the history of the moth and the subsequent literature. On seeing the long spur of *A. sesquipedale*, Darwin predicted that its pollinator would be a moth with a long proboscis. For more than a century following Darwin’s prediction this was assumed to be the case. The pollinator was taken to be *Xanthopan morganii praedicta*, despite the fact that it had not been observed to visit *A. sesquipedale* flowers. Direct observations, infra-red cinematography and photographs published between 1993 and 1997 and a video made in 2004, all of which show *X. morganii praedicta* visiting *A. sesquipedale* flowers and removing pollinia, proved that Darwin’s prediction was accurate. Recent research suggests that selection pressure exerted by predators on the pollinators, resulted in the evolution of extreme tongue lengths and a special hovering flight. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 403–432.

ADDITIONAL KEYWORDS: Angraecinae – co-evolution – Madagascar – Orchidaceae – pollination – sphingid moths – Wallace.

INTRODUCTION

On 25 January 1862 Charles Darwin (1809–1882) received a box of orchids from James Bateman (1811–1897), a well-known orchid grower, not from a collector in Madagascar as suggested in a popular biography (Moore, 1957). The names of the orchids were not included, and Darwin could not identify some. He wrote to Bateman, perhaps on the same day or on the 26th (the letter has not been found; footnote 2 in Bateman, 1862a and footnote 2 in Bateman, 1862b) inquiring about their identity. Bateman’s third son, Robert (1842–1922), who became a wealthy property owner as well as an artist and botanical illustrator, replied on 28 January 1862 because his father was ‘obliged to leave home early’ (Bateman, 1862a)

and indicated that the package contained *Zygopetalum crinitum* Lodd., *Odontoglossum bicktoniense* (Bateman) Lindl., *Odontoglossum pulchellum* Bateman ex Lindl., *Calanthe vestita* Wall. ex Lindl., *Laelia anceps* Lindl. and *Angraecum sesquipedale* Thouars. James Bateman wrote on 1 February 1862 stating that he ‘was very glad . . . that the orchids were so acceptable’ and added ‘Pray forgive my gardener’s carelessness in omitting the names; when I charged him with the misdemeanor he defended himself on the ground that he could never have supposed you could have been ignorant of them!’ (Bateman, 1862a). [This review will contain a large number of direct quotations, some of them extensive, due to the: (1) nature of the events being described; (2) individuals involved; and (3) age and uniqueness of the original literature and an effort to retain the flavour of the times, literature, events and locales].

*Corresponding author. E-mail: jarditti@uci.edu

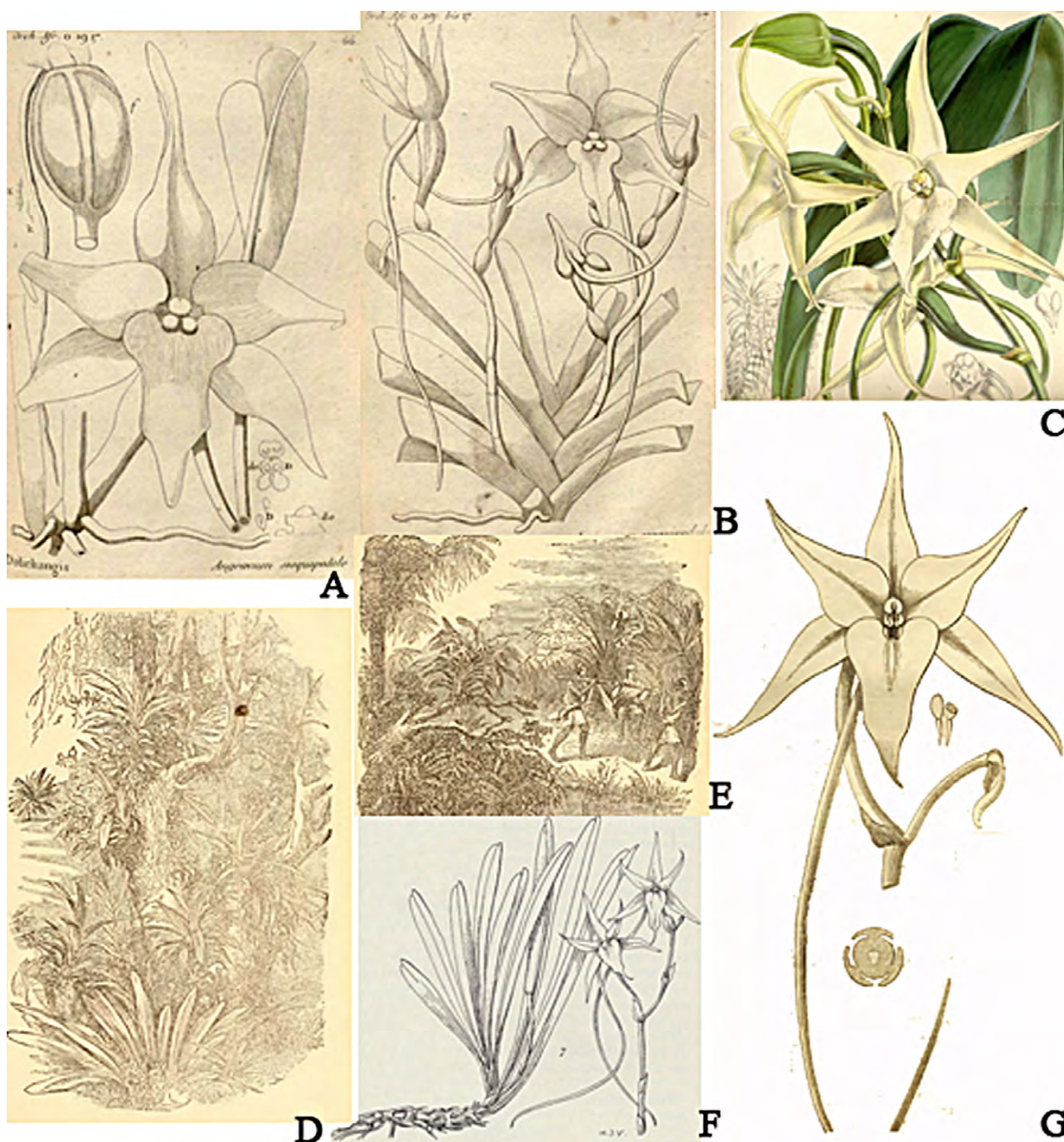


Figure 1. *Angraecum sesquipedale*. Bateman, A, B, the first illustrations of *Angraecum sesquipedale* (du Petit Thouars, 1822); C, painting of what is probably the second flower of *Angraecum sesquipedale* to bloom in Britain (Anonymous, 1859); D, *Angraecum superbum* on a tree in Madagascar (Ellis, 1858); E, *Angraecum sesquipedale* on a tree branch in Madagascar (Ellis, 1858); F, *Angraecum sesquipedale* (Perrier de la Bâthie, 1941); G, line drawing of what may be the first flower of *Angraecum sesquipedale* to be seen in Britain (1857).

Regardless of whether Darwin was or was not ignorant of some or all of the orchids, he liked the contents of the package and was especially taken by the flowers of *A. sesquipedale* [(Figs 1A–C, F, G, 2A–C, 3A,

B, 4Ba, Ca). Several images of *A. sesquipedale* are included in this review in an effort to show: (1) the very flowers which are part of this account; and (2) floral details and several forms of this orchid. Several



Figure 2. *Angraecum sesquipedale*. A, flower of *Angraecum sesquipedale* photographed from roughly the same distance as that at which a pollinating moth would be positioned (one of a series of photographs taken in J. Arditti's laboratory in the 1970s); B, *Angraecum sesquipedale* flowers on a plant in China (courtesy Dr Perner Holger); C, painting of *Angraecum sesquipedale* from one of the most magnificent illustrated orchid works in the late 1800s, *Reichenbachia*, after the species became more commonly available in the UK (Sander, 1888); D–F, *Angraecum sesquipedale* seeds, scale bar = 1 mm (courtesy Troy Meyers, Meyers Conservatory, <http://www.troymeyers.com>).

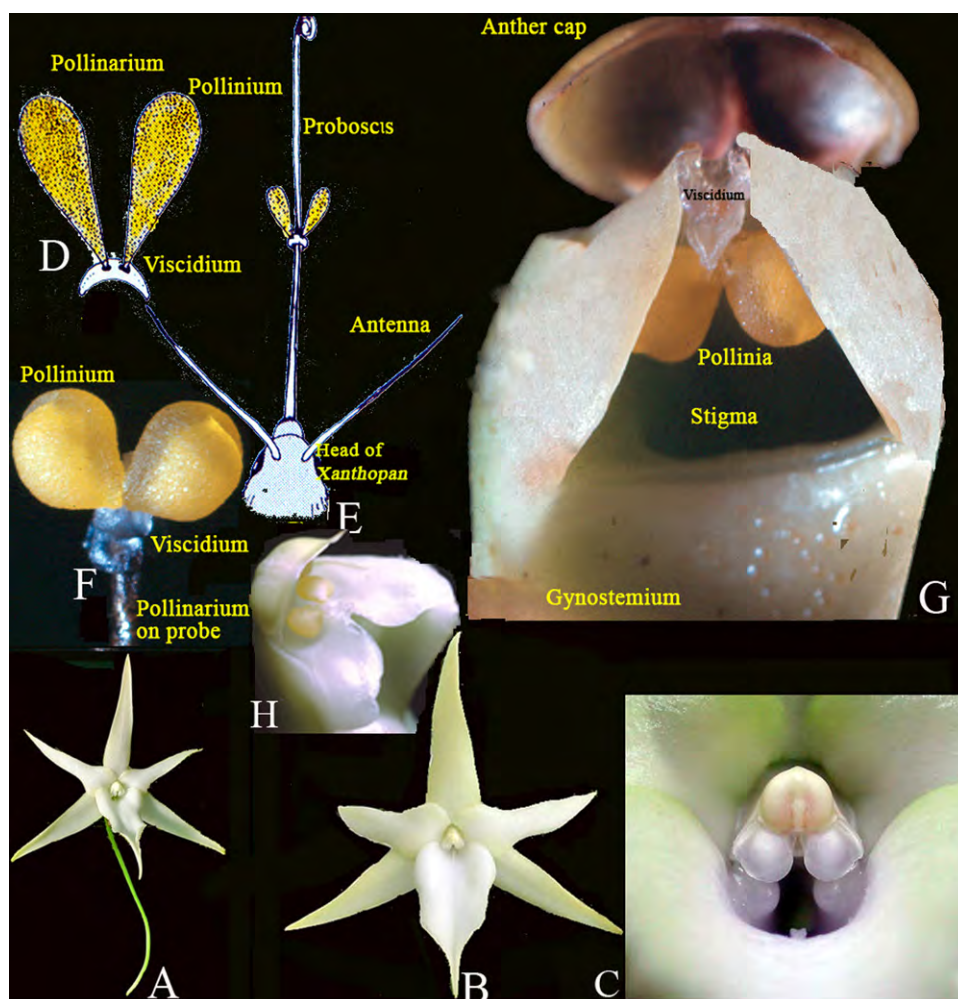


Figure 3. Pollinaria, stigma and entrance into spur of *Angraecum sesquipedale*. A–C, successively closer views of the anther cap and entrance into spur (courtesy Hans-Joachim Włodarczyk, Großbräschener Orchideen, W.-Seelenbinder-Str. 21, 01983 Großbräschchen, Germany, <http://www.orchideenwloдаряk.de>); D, a pollinarium showing pollinia and viscidium; E, pollinarium on the proboscis of *Xanthopan*. D and E are electronic modifications of a somewhat faded painting, now lost, which hung for years in the coffee room of the Department of Botany at the National University of Singapore before it moved from the old Bukit Timah campus to be merged with the Zoology Department to form an Institute (now a Department) of Biological Sciences at Kent Ridge; F, pollinarium on a teasing needle; G, the pollinaria in H inserted into the spur opening by simulating the proboscis movement of a moth; H, lifted anther cap to show pollinia on top of the rostellum (F–H, from a series of photographs taken in J. Arditti's laboratory in the 1970s).

illustrations of *Xanthopan morganii* and *X. morganii praedicta* are also included to show that there is variability within the species and subspecies. Some illustrations of orchids and moths are of low quality. The reason for this is the low quality of the originals. On 25 January 1862 Darwin wrote his friend, Joseph Dalton Hooker (1817–1911), Director of the Royal Botanic Gardens, Kew, twice, that he received *Angraecum sesquipedalia* (*sic*; Darwin, 1862b) and *A. sesquipedale* flowers from Bateman (Darwin, 1862c). The letters, written before Robert Bateman's reply, indicate that: (1) the *Angraecum* (Darwin wrote

Angraecum) flowers really excited Darwin; (2) he marvelled both times at the length of the nectary; and (3) Bateman's gardener, perhaps a Mr Sherratt (Cribb & Tibbs, 2004), was right in assuming that Darwin would know the orchids.

Darwin's fascination with *A. sesquipedale* led him to suggest 'a kind of an arms race' (Micheneau, Johnson & Fay, 2010) or a 'feedback loop' (Fay & Chase, 2009) which results in *Angraecum* spp. and flowers 'with ever longer spurs and hawkmoths with ever longer tongues' (Fay & Chase, 2009; Micheneau *et al.*, 2010). By making this suggestion Darwin made

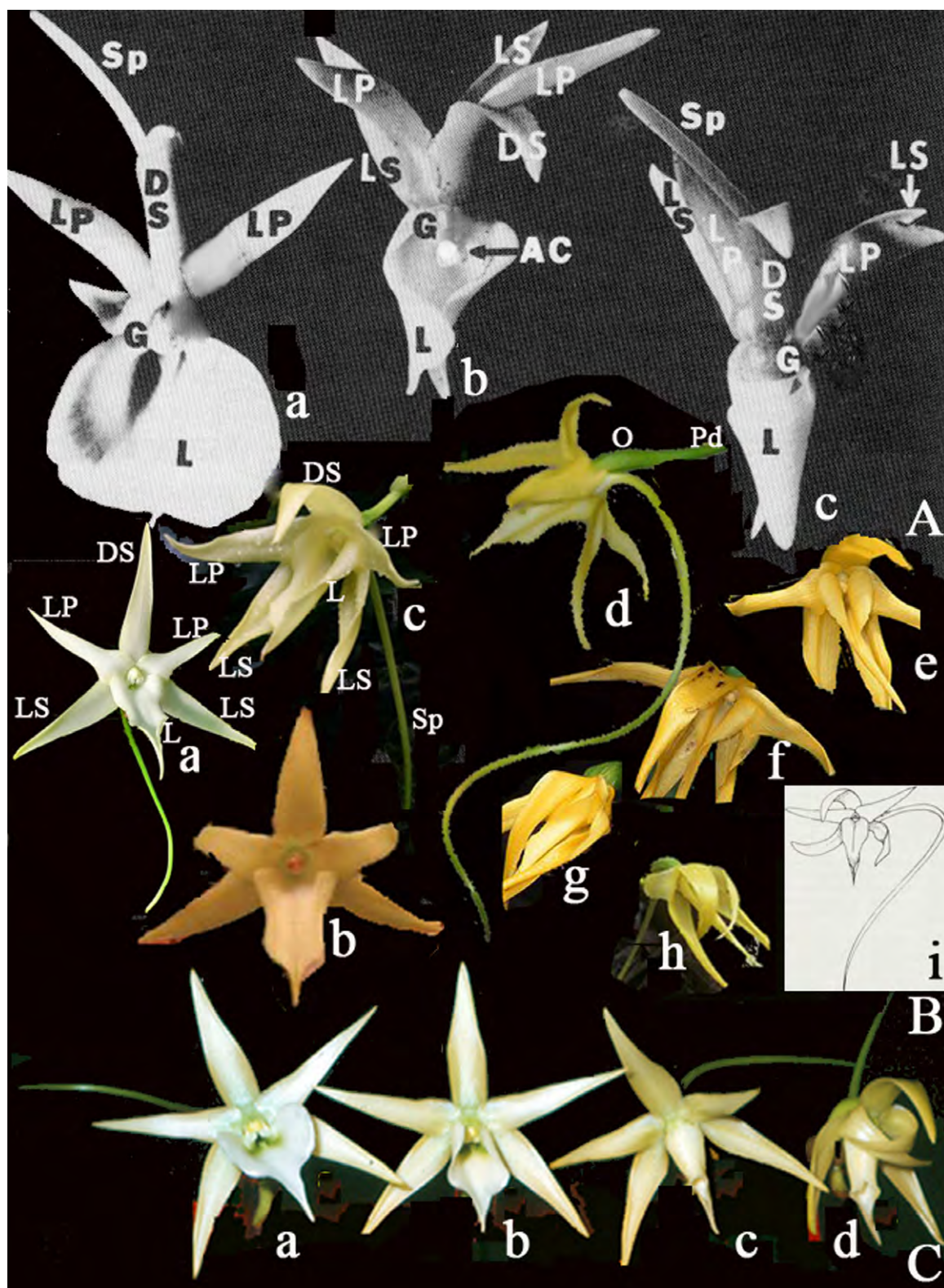


Figure 4. Postpollination movement of *Angraecum* perianth segments. A, a–c, *Angraecum eburneum* Bory; B, a–i, *Angraecum sesquipedale*; C, a–d, *Angraecum Veitchii*, a hybrid between the two species. Abbreviations: AC, anther cap; DS, dorsal sepal; G, gynostemium (column); L, labellum (lip); LP, lateral petal; LS, lateral sepal; O, ovary; PD, pedicel; Sp, spur (courtesy Dr Michael S. Strauss and part of a series of photographs taken in J. Arditti's laboratory in the 1970s).

one of his major contributions to evolutionary biology: coevolution (Micheneau *et al.*, 2010). This review will concentrate on Darwin's prediction of a pollinator for *A. sesquipedale*, the moth he predicted, the coevolution between the two and the scientists who studied them.

ANGRAECUM SESQUIPEDALE

In a family known for striking flowers, those of *A. sesquipedale* (Figs 1A–C, F, G, 2A–C, 3A, B, 4Ba, Ca) are among the most spectacular (Lecoufle, 1982; Hillerman & Holst, 1986; Du Puy *et al.*, 1999; Motes, 2011; Sawyer, 2011). The species is native to the Madagascar lowlands (du Petit-Thouars, 1822; Ellis, 1858; Perier de la Bâthie, 1930, 1941, 1981; Hillerman & Holst, 1986; Du Puy *et al.*, 1999; Anonymous, no date). It is primarily an epiphytic and rarely a saxatilis or semi-terrestrial species (Perrier de la Bâthie, 1941, 1981; Anonymous, no date). Its generic name is derived from the Malay word for orchid, *angurek* (Schultes & Pease, 1963); currently, *angrek*, *ang-gerek* or *anggerik*. The specific epithet is a combination of the Latin word *sesqui* (one and a half) and *pedalis* (one foot long) which means foot and a half long or wide (Stearn, 2004). In Madagascar the plants flower from June to September whereas when grown in England and Europe they bloom in mid-winter (Anonymous, 1866) or roughly between December and January (Anonymous, no date). More generally, in the northern hemisphere flowers are produced from October (rarely) to May (Hamilton, 1990).

FIRST DESCRIPTION

Louis-Marie Aubert-Aubert du Petit-Thouars (1756 or 1758–1831) and his brother Aristide Aubert-Aubert du Petit-Thouars (1760–1798) wanted to hire a ship three years after the start of the French Revolution (1789–1799) and leave France on 22 August 1792. Their plan was to search for the lost La Pérouse expedition which had not been seen after leaving Australia on 10 March 1788 for New Caledonia, the Santa Cruz Islands, the Solomon Islands, the Louisiade Archipelago and the western and southern coasts of Australia (du Petit-Thouars, 1834; Jacquet, 2002, 2007). However, Louis-Marie was delayed, having been arrested by revolutionaries, tried and fortunately acquitted. He left France in October 1792 and arrived in Mauritius in May 1793. After that he spent 10 years in the French Indian Ocean islands including three and a half years on La Réunion and one year in Madagascar. During that time he collected plants and sent them to Antoine Laurent de Jussieu (1748–1836) and Jean-Baptiste Pierre Antoine de Monet, Chevalier de la Marck (1744–1829; often known as Lamarck, the originator of the theory of

inheritance of acquired characters as a mechanism of evolution).

On his return to France in 1802 du Petit-Thouars brought back about 2000 specimens and 600 drawings. He used these to publish his best known work, *Histoire Particulière des Plantes Orchidées Recueillies sur les Trois Isles Australes d'Afrique* (du Petit-Thouars, 1822, 1979), which contains descriptions of 91 species and includes good quality line drawing monochrome plates. One of the species (plates 66 and 67) is *A. sesquipedale* (Fig. 1A, B), discovered in 1798, for which du Petit-Thouars coined the specific epithet in allusion to the very long spur (Anonymous, 1857). He did not introduce any *Angraecum* plants into cultivation.

INTRODUCTION INTO CULTIVATION

For 35 years after the publication of du Petit-Thouars' book, it was 'the anxious wish of Europeans to procure [*A. sesquipedale*] for cultivation' (Anonymous, 1857), but they could not because the plant was 'as difficult to import as . . . to propagate' (Anonymous, 1866). The reasons for its 'great rarity' included internal strife in Madagascar starting in 1828, an attempt at gun boat diplomacy by the British and French in 1845, a cessation of 'all amicable intercourse . . . for eight years' starting in 1848 (Ellis, 1858) and the long voyage around the Cape of Good Hope which resulted in the death of many plants (Anonymous, 1866). In fact, no plants were taken to the United Kingdom or anywhere else until 1857 (Anonymous, 1857; handwritten note on a painting by John Day in Cribb & Tibbs, 2004).

Early in 1853, the Reverend William Ellis (1794–1872) was invited 'to proceed to Madagascar, on a visit of friendship' (Ellis, 1858). He left Southampton on 14 April 1853 and arrived in Madagascar on 18 July of the same year. After that he visited Madagascar twice more (1854 and 1856), left for the last time on 18 November 1856 and wrote a book about his travels (Ellis, 1858) which became popular. He observed both *Angraecum superbum* Thouars and *A. sesquipedale* on his second visit and illustrated them (Fig. 1D, E; he carried a camera while in Madagascar, but a collection of his photographs, now at the Getty Museum, does not include any of orchids). His description of *A. sesquipedale* suggests that he also collected plants on the second trip: it was 'most abundant and beautiful . . . they grew most plentifully on trees of thinnest foliage . . . high up amongst the branches, often throwing long straggling stems terminating in a few small, and often apparently shrivelled, leaves. The roots also partook of the same habit. They were seldom branched or spreading, but long, tough, and single, sometimes running down the branch or trunk of a tree, between fissures on the rough bark, to the length of twelve or fifteen feet [3.6–4.5 m]; and so tough and tenacious

Table 1. Price of one *Angraecum sesquipedale* plant in 1862–1880 (Cribb and Tibbs, 2004)^a

Sale	Year	Conversion to 2010 value using price index [†]		Annual income, £s 1860–1880 [†]		Income conversion to 2010 £ value using average earnings [‡]	
		Price, £	Price, £	Labourer	Skilled	Labourer	Skilled
John Day to Benjamin Williams	1862	20	1,460	28 16 s	71 3 s	17,200	42,400
John Russell to [] Philbrick	1875	24 4 s	1,780	36 8 s	91 10 s	15,940	39,900
At auction	1880	19	1,480	35 9 s	91 10 s	14,900	38,500

^aOn each row the price of a single plant is given for the year stated, and that value is converted to the 2010 value (latest available) based on the retail price index changes over that period. This occupies the first 4 columns. In the last 4 columns are given the annual average income for a labourer and a skilled worker respectively, for the period 1860–1880, calculated as at 1870, together with those values converted to 2010 values on the basis of changes in average earnings over the period 1870–2010. Reported sums are rounded to the nearest shilling. Annual income was calculated from daily wages allowing 305 working days year⁻¹ [365–(52 Sundays and 8 holidays)]. Before the pound was made decimal £1 = 20 shillings (s) and 1s = 12 pence (d). On 01 April 2012 £1 = US\$1.60.

[†]Sources: L. H. Officer and H. Williamson. 2011. Five ways to compare the relative value of a UK pound amount, 1830 to present at <http://www.measuringworth.com/ukcompare/result/php> and <http://privatewww.essex.ac.uk/~alan/family/N-Money.html>. Some information was kindly provided by Prof. Brian Ford.

that it required considerable force to detach or break them' (Ellis, 1858).

A description of the first plant to flower in Britain (Anonymous, 1857) also points to the second visit as the occasion of collection and dispatch of plants to England: 'The Rev. Mr. Ellis . . . met with it about 2½ years ago in the forest of that island, and having succeeded in sending home three plants in a living state one of them flowered magnificently' (Fig. 1G). Ellis's wife and his grower, Mr Gedney (Cribb & Tibbs, 2004), are not credited with bringing the plant to flower but should have been because Ellis was on 'renewed absence from England when Mrs. Ellis favoured [*The Gardeners' Chronicle*] with a flower for examination, and an extremely clever sketch [Fig. 1G]' (Anonymous, 1857). Subsequently Ellis provided John Lindley (1799–1865) with a description of the species in its native habitat, which included wording about the roots that is the same as above except for the length which is given as '12 or 18 feet [3.6–5.4 m] or more' (Anonymous, 1857).

In 1857 all plants of *A. sesquipedale* in England were owned by the Rev Ellis 'with the exception of one communicated by him to Mr. Veitch' (Anonymous, 1857). The fate of this plant is not known. It is not even mentioned by James Veitch & Sons in their discussion of the species (Veitch & Sons, 1887–1894). The second plant owned by Ellis flowered in February 1859 (Fig. 1C). In describing the plant, Sir William Jackson Hooker (1785–1865) stated that the flowers are sometimes as long as the plants themselves and they do not exceed two feet in height (Anonymous, 1859). *Angraecum sesquipedale* continued to be extremely

rare in cultivation (Anonymous, 1857, 1859, 1866; Veitch & Sons, 1887–1894) until after the opening of the Suez Canal in 1869 (Veitch & Sons, 1887–1894; Sander, 1888; Rolfe, 1901). Therefore, it is not surprising that plants sold for very high prices (Table 1).

DESCRIPTION OF THE SPECIES

The descriptions and illustrations of *A. sesquipedale* in *Histoire (du Petit-Thouars, 1822)* and *Three visits to Madagascar* (Ellis, 1858) provide interesting information and are historically valuable, but neither provides details of the kind appropriate to a taxonomic work. Such details became available in 1941 (Perrier de la Bâthie, 1941, 1981).

Henri Perrier de la Bâthie (1873–1958) spent much of his life in Madagascar (1896–1933 except for military service in 1914–1918) before returning to France and becoming Director of Research at the Centre National de la Recherche Scientifique (Leandri, 1962; Jacquet, 2002, 2007). He wrote about orchids in a volume entitled *49^e Famille.—orchidées*, which is part of *Flore de Madagascar* edited by his friend Henri Jean Humbert (1887–1967; sometimes listed as Jean-Henri Humbert). He also made major contributions to Rudolf Schlechter's treatment of the orchids of Madagascar, which was appropriately entitled *Orchidaceae Perrierianae* (Schlechter, 1925). Schlechter also named 29 orchid species in 24 genera and the genera *Perrierella* Schltr. and *Neobathiea* Schltr. in his honour (Jacquet, 2002). In turn, de la Bâthie named three species in three genera in Schlechter's honour (Jacquet, 2002).

In *Flore de Madagascar* (Perrier de la Bâthie, 1941, 1981), *A. sesquipedale* (Fig. 1F; also see Figs 1A–2C, 1G, 2A–C, 3A, B, 4Ba, Ca) is described as having ‘stems . . . always shorter than the leaves; leaves [not] rigid . . . 25–30 cm long, unequally bilobed . . . Inflorescences 1–3 flowered, shorter than the leaves; peduncle 10–12 cm; bracts generally . . . a quarter of the length of the pedicel; flowers pure white, very large . . . [segments] 7–9 cm long . . . Sepals oval-acuminate, 2 cm wide . . . Petals of the same form, but slightly shorter (7–8 cm) and slightly wider (2.5–2.8 cm). Labellum 6.5–8 cm long, concave and pandurate, 3.5–4 cm wide above the base and 18–24 mm in the upper third . . . with 2 large calluses on the sides of the spur orifice . . . spur 30–35 cm long . . . Column thicker (10 mm) than tall (6 mm) . . .’ (Perrier de la Bâthie, 1981). Spur length has also been reported to be 30 cm (Denso, 1943). More recent measurements are (see Table 4): length 33.3 ± 4.6 cm ($N = 15$) with the range being 27–43 cm (Wasserthal, 1997). As in other hawkmoth-pollinated orchids the spurs contain nectar composed of several sugars (Table 2). Not described are the seeds, which are small like those of other orchids (Fig. 3D–F).

A somewhat smaller form of *A. sesquipedale* from Fort Dauphin was described as *A. sesquipedale* var. *angustifolium* Bosser & Morat (Bosser & Morat, 1972). Another small form based on a greenhouse plant was named *A. bosseri* Senghas (Senghas, 1973), but this is now considered to be a synonym of *A. sesquipedale* var. *angustifolium*.

Flowers (Hillerman & Holst, 1986) are greenish when they open, but turn white within 1–3 days and then become creamy (the sequence is Figs 1C, 2A–C, 3A, B, 4Ba). Like the blossoms of many orchids the flowers are long lived and can remain fresh for up to 40 days (Arditti, 1992). On ageing or after being pollinated floral segments turn yellow (in the following sequence: Fig. 4Bb–Bh) and the petals ‘move slightly forward to a position approximately equiplanar to each other’ (Strauss & Koopowitz, 1973; Strauss, 1976). Sepal movement is in the same direction, but more pronounced. This places them below the labellum and parallel to it. These movements cause the star shape of the flowers to disappear. They continue until the flower becomes a small yellow bundle (Fig. 4Bg, Bh). The labellum moves little if at all. In the related species, *A. eburneum* Bory the three sepals and two lateral petals move minimally whereas the labellum curls inward (Fig. 4Aa–Ac). This also changes the initial shape of the flower (Strauss & Koopowitz, 1973; Strauss, 1976). These movements are obviously species specific. The post-pollination movements of the two species are passed to their hybrid, *Angraecum Veitchii* (Fig. 4Ca; Strauss & Koopowitz, 1973; Strauss, 1976); both its sepals

and petals, including the labellum, fold inward (Fig. 4Cb–4Cd).

The fragrance of *A. sesquipedale* is produced during the evening and night. It has been described as ‘very spicy, masculine [! *sic*] and sometimes overpowering’ (Hillerman & Holst, 1986), ‘strong’ (Frownie, 2005), ‘pronounced’ (M. S. Strauss, USDA, pers. comm.) and simply as jasmine-like and/or good or pleasant which can easily fill a room or a greenhouse. It contains 40 identified components (Kaiser, 1992, 1993; Table 3). The scent ‘disappeared’ shortly after the flowers folded following pollination or auxin application to stigmas (M. S. Strauss, 1976, pers. comm.).

DARWIN

In a letter to J. D. Hooker dated 25 January 1862, Darwin wrote, ‘I have just received such a Box full from Mr Bateman with the astounding *Angraecum sesquipedalia* [*sic*] with a nectary a foot long. Good Heavens what insect can suck it’ (Darwin, 1862a). In their letters to Darwin (Bateman, 1862a, b), neither James Bateman nor his son Robert mentioned the source of their plant. However, as all plants of *A. sesquipedale* in England at that time had been imported by Ellis (Anonymous, 1857, 1859, 1866), it is reasonable to assume that Bateman owned a plant imported by Ellis or a division from it. Therefore, the flowers Darwin received must have resembled or were the same as those which flowered in 1857 and 1859 (Fig. 1C, G). Given the rarity of the species and the high cost of plants, James Bateman’s gift of several flowers to Darwin was a generous gesture, which Darwin acknowledged both on pages 197 (text) and 58 (footnote) of the first edition of *Contrivances* and on pages 105 and 162 of the second edition (Darwin, 1862a, 1904). It is a credit to Darwin that he discussed the flowers and their possible pollinator in the first edition despite receiving them only 3 months and 22 days before its publication on 15 May 1862 (Darwin, 1958).

FLOWER STRUCTURE

As he did with many other orchids, Darwin examined the column carefully and noted that ‘the rostellum is notched [Figs 3C, 5Bb2, Bb3, Bc1, Bc2] and two separate membranous disks can be removed, each carrying by a short pedicel [now called the stipe or caudicle] its pollen mass [Fig. 5Ba, Bb1, Da1–Da3]’ (Darwin, 1862a: 186; 1904: 154). He continued with the description of the rostellum several pages later (Darwin, 1862a: 198; 1904: 162), ‘The rostellum is broad and foliaceous [Fig. 3C, G, H] and arches rectangularly over the stigma [this can be inferred to some extent from Fig. 3, but appears more like a

Table 2. Nectar properties of some angrecoïd and hawkmoth-pollinated orchids*

Species	Sugar concentration (%)	Spur length/height of nectar column (cm)	Volume (µL)	Sugars		Reference(s)
				Kinds	Energy (mg J ⁻¹)	
<i>Aerangis brachycarpa</i>		15.9/14.2	20.2			Martins & Johnson (2007)
<i>Aerangis confusa</i>		4.5/3.9	6.9			
<i>Aerangis thomsonii</i>		13.5/4.1	14.9			
<i>Aerangis verdickii</i>	flowers reabsorb nectar after pollination					Koopowitz & Marchant (1998)
1994, virgin	14.4	na/23.6				
naturally pollinated	3.2					
1995, virgin	18.3					
naturally pollinated	8.7					
virgin	13.8		19			
48 h after pollination	4.3					
Emasculated		na/25.1				
Pollinated		na/24.3			684.2	
Per plant				F, G, S		Jeffrey, Arditti & Koopowitz (1970)
<i>Angraecum comorense</i>						Darwin (1962a)
<i>Angraecum sesquipedale</i>		29.2/3.8				Jeffrey <i>et al.</i> (1970)
<i>Angraecum eburneum</i>				F, G, R, S		Jeffrey <i>et al.</i> (1970)
<i>Angraecum sesquipedale</i>				F, G, R, S M(?)		Wasserthal (1997)
<i>Angraecum sesquipedale</i>	16.5±4	27–43/7–25	40–300			Wasserthal (1997)
<i>Angraecum sororium</i>	2.8–14.7	16.9±5.98	165 ± 89.91			Jeffrey <i>et al.</i> (1970)
<i>Angraecum Veitchii</i>		24.9–26.9/10.1–17	66–182			Micheneau <i>et al.</i> (2010)
Hawkmoth-pollinated orchids	15.2	4.6–33.3/na		F, G, S R(?)		
<i>Mystacidium venosum</i>	16	2.5–5.5/na	1.8			Luyt & Johnson (2001, 2002)
	The flowers of this species reabsorb nectar after pollination			F, G, S 10:3:87		
<i>Rangaris amaniensis</i>		15.6/9.1	9.9			Martins & Johnson (2007)

*F, fructose; G, glucose; M, melezitose; na, not available; R, raffinose; S, sucrose.

Table 3. Components of the *Angraecum sesquipedale* fragrance (Kaiser, 1992, 1993)*

Compound	GCMS spikes, percent of area
Anis aldehyde	m
Anisyl acetate	m
Anisyl alcohol	m
Benzaldehyde	1.6
Benzyl acetate	1.1
Benzyl alcohol	14.8
Benzyl benzoate	3.0
Benzyl butyrate	m
Benzyl isovalerate	m
Benzyl salicylate	1.0
(E)-Cinnamic alcohol	m
Dihydroactinidiolide	m
Ethylbenzoate	m
Geranial	m
Geraniol	m
Geranyl acetate	m
(Z)-3-Hexenol	m
(Z)-3-Hexenyl benzoate	m
Hydroxyquinone dimethyl ether	m
Indole	m
β -Ionone	m
β -Ionone epoxide	m
Isoamylacetate	m
Isoamyl alcohol	1.0
Isovaleraldehyde	2.5
Isovaleraldoxime (E/Z approx. 2.1)	34.0
Isovaleronitrile	3.5
Limonene	m
Linalool	m
cis-Linalool oxide (pyranoid)	m
trans-Linalool oxide (pyranoid)	m
Methyl antranilate	m
Methyl benzoate	17.9
Methylsalicylate	m
p-Methoxy cinnamic alcohol	m
Neral	m
Phenylacetaldehyde	m
Phenylacetaldoxime	2.0
Phenylethylalcohol	2.5
Phenylethylbenzoate	m

*m, minor.

triangle in Figs 3G, H, 5Bb, Bc] and over the orifice of the nectary [Figs 3C, G, 5Bb, Bc]; it is deeply cleft enlarged or widened at the end [Figs 3C, G, 5Bb, Bc]. Hence the rostellum pretty closely resembles . . . that of *Calanthe* [R.Br.] after the disk was removed [Fig. 5C]. The under surfaces of both margins of the cleft near its end are bordered by narrow strips of viscid membrane, easily removed so that there are

two viscid discs [Fig. 5Bb1, Da1–Da3]. To the middle of each disk a short membranous pedicel is attached; and each carries at its other end a pollen mass [Fig. 3F, Bb1, Da1–Da3]. Below the rostellum, a narrow, ledge-like viscid stigma is seated [Figs 3A–C, G, H, 5Ba, Bb2, Bb3, Bc1, Bc2]’ (Darwin, 1862a, 1904; the wording in both editions is identical in all these quotations).

The nectary of *A. sesquipedale* (Figs 1A–C, F, G, 2A–C, 3A, 4Ba–Bd, Bf, Bi, 5A, 8B, D, 10A, B, E, F) astounded Darwin. The contents of the nectary (Table 2) also interested him: ‘In several flowers sent me by Mr. Bateman I found the nectaries eleven and a half inches [29.2 cm] long, with only the lower inch and a half [3.8 cm] filled with very sweet nectar’ [‘with nectar’ in the second edition (Darwin, 1904)].

REVIEWS OF *CONTRIVANCES*

A spur of such length (Figs 1A–C, F, G, 2A–C, 3A, 4Ba–Bd, Bf, 5Bi, A, 8B, D, 10A, B, E, F) is certain to draw attention and require an explanation and Darwin provided one (see below). Darwin wrote that his explanation was ridiculed (by ‘some entomologists’) only in the second edition (i.e. he referred to comments made after 15 May 1862, the publication date of the first edition of *Contrivances*). If ridicule was published we could not find it in the publications we consulted.

The Athenaeum, a magazine of letters, arts and sciences in the UK, treated the book ‘with very kind pity and contempt’ even if the ‘reviewer knew nothing of his subject’ (Darwin, 1958). About half the review (Anonymous, 1862c) consisted of an overview of orchids in general, much of it direct quotes from Darwin and the rest disparaging remarks. There is nothing specific in this diatribe. *Angraecum sesquipedale* and the moth prediction are not mentioned. Darwin was right about the reviewer being ill informed. It seems that his sole purpose was to attack Darwin and his ideas. From a present perspective he failed and actually made a fool of himself, but at the time Darwin was concerned that ‘the *Athenaeum* [review] will hinder sales greatly’ (Darwin, 1862d). It is impossible at present to determine if this review affected sales. There were other criticisms, but they were limited, scholarly and polite, even if driven by ideology and religion rather than science. Most of the reviews were laudatory, as are recent comments (Motes, 2011; Sawyer, 2011).

When not dealing with politics and governmental matters, George Campbell (8th Duke of Argyll, 1823–1900) dabbled in science and economics and was a leader and publicist in the opposition to Darwinism. In his latter capacity he devoted almost ten pages in a book (Campbell, 1884) to *Contrivances* and to Alfred

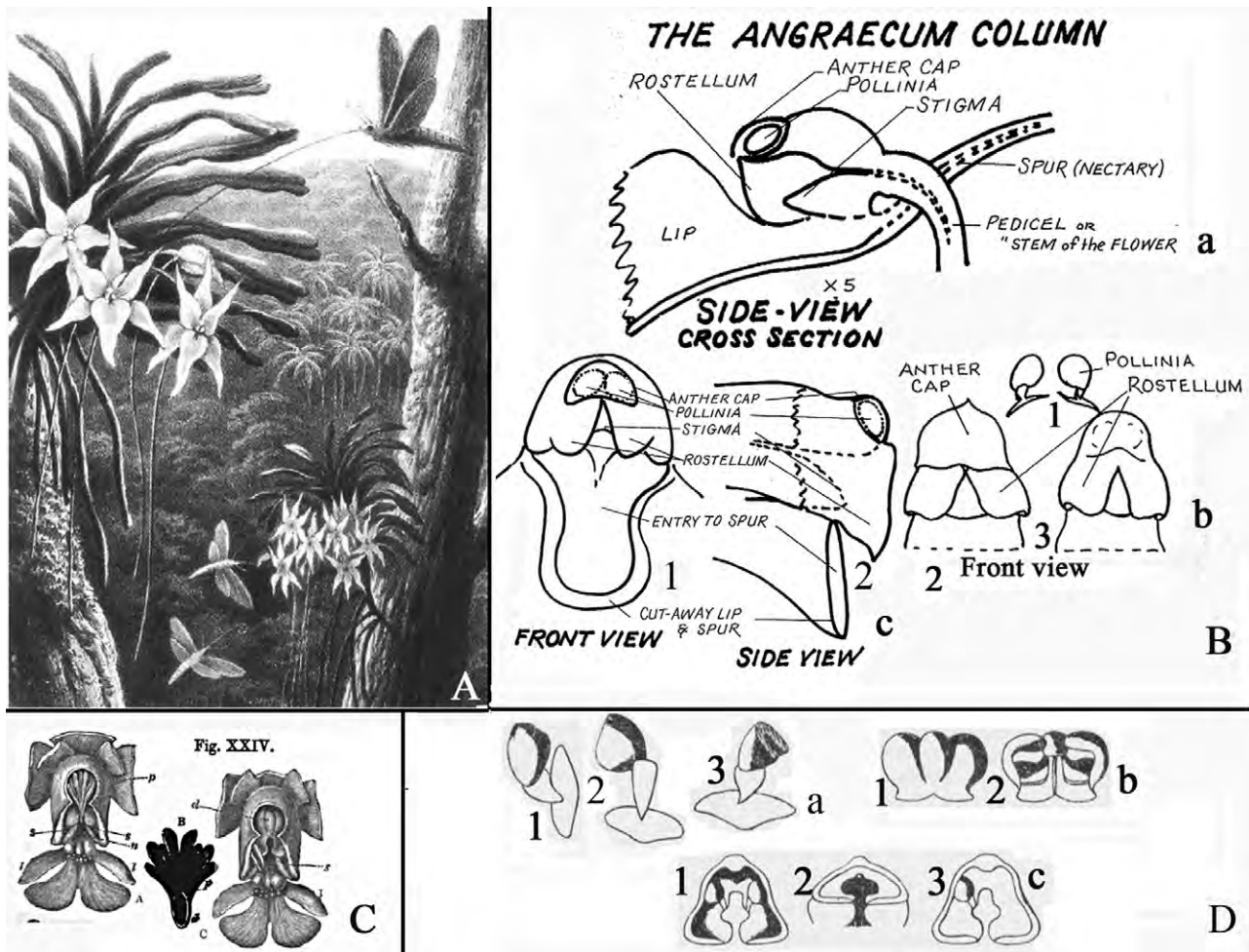


Figure 5. Pollination and floral structure. A, an artist's conception of *Angraecum sesquipedale* pollination by a moth with a long proboscis (Wallace, 1867a); B, *Angraecum* column (courtesy Walter Upton); C, *Calanthe masuca*. Original explanation of symbols rearranged in alphabetical order: A, flower viewed from above, with the anther-case removed, showing the eight pollen-masses in the proper position within the clinandrium. All the sepals and petals have been cut away except for the labellum. B, pollen masses attached to the viscid disc, seen from the underside. C, flower in the same position as in A, but with the disc and pollen-masses removed, and now showing the deeply notched rostellum and the empty clinandrium in which the pollen-masses lay. Within the left-hand stigma two pollen-masses can be seen adhering to its viscid surface. cl., in Figure C, clinandrium, the pollen-masses being removed; d., viscid disc; l., labellum; n., mouth of the nectary; p., pollen-masses; s.s., the two stigmas (Darwin, 1904). D, pollinia and rostellum. a, single pollinium in different positions (1, 2). One of them is cut (3) to show that it is furrowed. b, an anther viewed from above (1) and below (2). c, three clinandria (referred to as androclina or anther bed in the original) one (1) with two pollinia, one (2) with no pollinia and one (3) with a single pollinium (Sander, 1888).

Russel Wallace's (1825–1913) support for the ideas expressed by Darwin (1867a). He wrote well, with erudition, understanding, some knowledge of the subject and respect for Darwin, but primarily as a creationist. Inevitably, he concluded that 'long before we have searched out all that the Natural includes, there will remain little in the so called Supernatural which can seem hard of acceptance' (Campbell, 1884). On the whole his criticism was that Darwin and Wallace did not refer to 'that function of power of

Mind which we know as Purpose and Design' because 'these purposes and ideas are not our own, but the ideas and purposes of Another – One whose manifestations are superhuman and supermaterial, but are not "supernatural" in the sense of being strange to Nature, or in violation to it' (Campbell, 1884). He did not ridicule Darwin's moth prediction. What Campbell seemed to argue for is the concept known at present as 'intelligent design'. He does it with finesse and scholarship, even if not convincingly. The Duke's

writings can also be read to imply that he saw Darwin as some kind of theological teleologist (Darwin was said to be a teleologist even more recently; Lennox, 1993), but Darwin's own writings made it clear that he saw the 'contrivances' of orchids as the result of natural selection. So, any teleology was selection-based and acutely antagonistic to theological teleology and creationism. *Contrivances* has also been viewed as a 'flank movement' against creationism and teleology (Beatty, 2006).

Another creationism-driven reaction to *Contrivances* was a lecture by David Moore (1807–1879), retired Director of the Glasnevin Botanical Gardens and the first person to report the germination of orchid seeds under horticultural conditions (Moore, 1849). *Angraecum sesquipedale* was not mentioned in the lecture (Moore, 1875) in which he complimented Darwin. It contained no ridicule and was centred on glorifying 'the boundless conceptions of the Creator' without specifically discussing *Contrivances*.

A two-pronged approach was taken by the *Journal of Horticulture, Cottage Gardener and Country Gentleman*. Its review of *Contrivances* was good even if it did not seem to favour 'Mr. Darwin's theory "on the origin of species"'. Straddling two worlds, the review concluded, 'As a contribution of the very highest order to the practical attainment of seedling of foreign Orchids [*sic*, *Contrivances* does not deal with seeds and seed germination], we would recommend the work, apart from all speculation about the origin and progress of the clothing of our planet' (Anonymous, 1862a). This review did not consider *A. sesquipedale* or Darwin's prediction of a pollinator. It contained no ridicule.

Miles Joseph Berkeley (1803–1889), a mycologist and, according to some, the founder of plant pathology, wrote a glowing, but unsigned, review of *Contrivances* for *The London Review* (Anonymous, 1862b; Darwin, 1862d; Hooker, 1862c) which did not ridicule Darwin's prediction of a moth that pollinates *A. sesquipedale*, and did not mix religion and science.

Hermann Crüger (1818–1864), a German pharmacist and botanist who was director of the Trinidad Botanical Gardens, corresponded with Darwin (Darwin, 1863b, c; Crüger, 1863a, b, c) about the pollination of Caribbean orchids and especially *Catasetum* Rich. ex Kunth. He also wrote a paper about orchid pollination (Crüger, 1864) which although not a review of *Contrivances* and *Origin* expressed his admiration for both. Crüger did not mention *Angraecum* and did not ridicule Darwin's prediction of a moth with a long proboscis.

William Bernhard Tegetmeier (1816–1912), a poultry, pheasant, bee and pigeon expert, who assisted Darwin in these areas (Richardson, 1916)

wrote a glowing review of *Contrivances* which was free of ridicule, mentioned moths but did not refer to *Angraecum* (Tegetmeier, 1862).

According to *The Saturday Review*, *Contrivances* was too technical but valuable (Anonymous, 1862d). The rest of the one-page review in this publication simply described a few of the contrivances Darwin enumerated in his book. Some of the language echoes what Darwin wrote about *Angraecum* and moths, but the review did not contain specifics or ridicule.

The review in *The Parthenon* (Anonymous, 1862e) was broader in scope and tried to relate some of the contents of *Contrivances* to Sprengel's book on pollination (Sprengel, 1793) and work by Robert Brown (without specifying which) and Hooker (without providing initials). This review was focused on European orchids and contained no ridicule.

William Alexander Forbes (1855–1883), a promising entomologist who died tragically in the Niger (the last entry in his journal was that he had high fever; Anonymous, 1883; Beddard, 1885), took Darwin's prediction seriously and suggested without ridicule that the moth 'would probably be Sphingidae of some kind, as no other moths would combine sufficient size and length of proboscis' (Forbes, 1873).

Wallace (1867a) replied to Campbell's criticism of Darwin's theory regarding the origin of long nectaries of *A. sesquipedale* and the long proboscis of his proposed pollinator. He wanted to do it 'satisfactorily to' Darwin (1867b) and did (Darwin, 1867b). His reply was a lucid elaboration of Darwin's theory (Wallace, 1867a). It included a remarkably accurate illustration of the still unknown, yet to be discovered moth with its proboscis inserted in a flower of *A. sesquipedale* (Fig. 5A). On the whole, the reply to Campbell was non-confrontational, and preserved mutual respect and cordiality (even as it demolished his arguments). So much so that Campbell's son was a pall bearer at Darwin's funeral.

Thomas Belt (1832–1878; naturalist and a Darwin supporter) criticized Wallace's account of the evolution of the nectary (as given in his book *Contributions to the Theory of Natural Selection*; Wallace, 1870: 272) on the grounds that it failed to consider adaptations which would prevent useless insects gaining access to the nectar, and was thus incomplete (Belt, 1874). However, Darwin addressed this criticism in the second edition of *Contrivances*, pointing out that 'the moth has to be compelled to drive its proboscis as deeply down as possible into the flower' which would mean that any moth trying to reach the unattainable nectar would be liable to pollinate the orchid anyway (Darwin, 1904: 165).

We have read correspondence between Darwin and Daniel Oliver (1830–1916; Oliver, 1862), George Bentham (1800–1894; Bentham, 1862; Darwin,

1863a), Charles Cardale Babington (1808–1895; Babington, 1862), Joseph Dalton Hooker (1817–1911; Darwin, 1862e, f; Hooker, 1862a, b, c), John Murray (1808–1892; Darwin, 1862d), Asa Gray (1810–1888; Darwin, 1862g) and James Samuelson (Darwin, 1867a; Samuelson, 1866). In all this correspondence *Contrivances* was mentioned and discussed, but never ridiculed.

Repeated references are made here to the lack of ridicule in reviews and comments because on page 163 of the second edition of *Contrivances* Darwin states that he was ridiculed for his belief that ‘in Madagascar there must be moths with proboscides capable of extension to a length of between ten and eleven inches [25.4–27.9 cm]!’ If such ridicule was published we could not find the publication(s) or letter(s) which contains it. This suggests the possibility that ridicule may have been verbal, perhaps friendly, in discussions between Darwin and entomological friends or colleagues. However, it most probably originated among the wider entomological community, of whom Darwin wrote to Charles Lyell, in the context of the spread of his theory, that ‘the entomologists alone are enough to keep [the] subject back for ½ a century’ (Darwin, 1863c).

XANTHOPAN MORGANII PRAEDICTA

What may be the earliest description of a moth which could be related to, or resemble, *Xanthopan morganii praedicta* was published in 1832 under the generic name *Amphonyx* by a Cuban zoologist named Felipe Poey y Aloy (1799–1891; Poey y Aloy, 1832). *Amphonyx* is now considered to be a synonym of *Cocytius* (Rothschild & Jordan, 1903). Another generic name, *Protoparce* (Burmeister, 1856), which was applied to Brazilian moths by the German entomologist Karl Hermann Konrad Burmeister (1807–1892) is also now a synonym of *Manduca*. In 1856 the controversial British Museum entomologist Francis Walker (1809–1874) erected a new genus *Macrosila*, now also a synonym of *Manduca* (Walker, 1856) and in it described *Xanthopan morganii* (Fig. 7A–C) as *Macrosila morganii*. He listed two specimens, one from Sierra Leone presented by the Rev. D. F. Morgan (about whom no information seems to be available) and another from the Congo provided by Sir John Richardson (1787–1865). It has been said that Walker was paid a shilling for every new species and a pound for each new genus and as a result produced sloppy and poor taxonomy. Actually Walker was paid a lump sum for every catalogue he wrote, but this may still not have been enough to ensure good work (http://www.ndsu.nodak.edu/ndsu/rider/Pentatomoidea/Biographical/biographical_W.htm).

Walker’s successor at the British Museum, Arthur Gardiner Butler (1844–1925), moved *Macrosila morganii* to *Protoparce* as *Protoparce morganii* (Butler, 1876). Finally, in 1903 Rothschild and Jordan established the genus *Xanthopan* (Rothschild & Jordan, 1903), and placed the moth variously known as *Amphonyx morganii*, *Macrosila morganii* and *Protoparce morganii* in the new genus as *Xanthopan morganii*. They also added a new subspecies, *Xanthopan morganii praedicta* (Figs 6A–E, 7D–F). The types for the new subspecies are a holotype male (Fig. 6D) in the collection of Oberthür, now at the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and a paratype female in the collection of Mabille, which is possibly also in the Carnegie Museum. The sources of the types were not stated (Rothschild & Jordan, 1903).

CLASSIFICATION OF *XANTHOPAN* *MORGANII PRAEDICTA*

The name and classification of *X. morganii praedicta* as a subspecies has survived for more than a century. However, questions remain regarding the relation of *Xanthopan* to tribe Acherotiini or the genera *Cocytius* and *Neococytius*, and also whether taxa with extremely long probosces form a monophyletic group or fall within a ‘reasonably compact clade’ (Kitching, 2002). A phylogenetic analysis based on the morphology of both adults and immature stages (Kitching, 2002) showed that: (1) hawkmoths with extremely long probosces do not form a monophyletic group and (2) the relationships of *Xanthopan* are ambiguous (Kitching, 2002). However, a more recent phylogenetic analysis based on DNA sequence data placed *Xanthopan* firmly with the *Cocytius* group (Kawahara *et al.*, 2009).

Despite several descriptions of *X. morganii morganii* and *X. morganii praedicta*, information on dimensions and weight is limited. The available information indicates that *X. morganii praedicta* is larger than *X. morganii morganii* and that females (at least of the former) are heavier (Table 4; Wasserthal, 1997). Photographs from Madagascar (Fig. 6A–E), The Gambia (Fig. 7D–F) and Gabon (Figs 6, 7) also suggest variability in a size and coloration within and between regions (Figs 6, 7 are included here to show this variability).

POLLINATION

The ‘Good Heavens what insect can suck it...’ phrase (Darwin, 1862b) has been cited so often that it is generally taken as being the prediction of *X. morganii praedicta*. However, the actual prediction

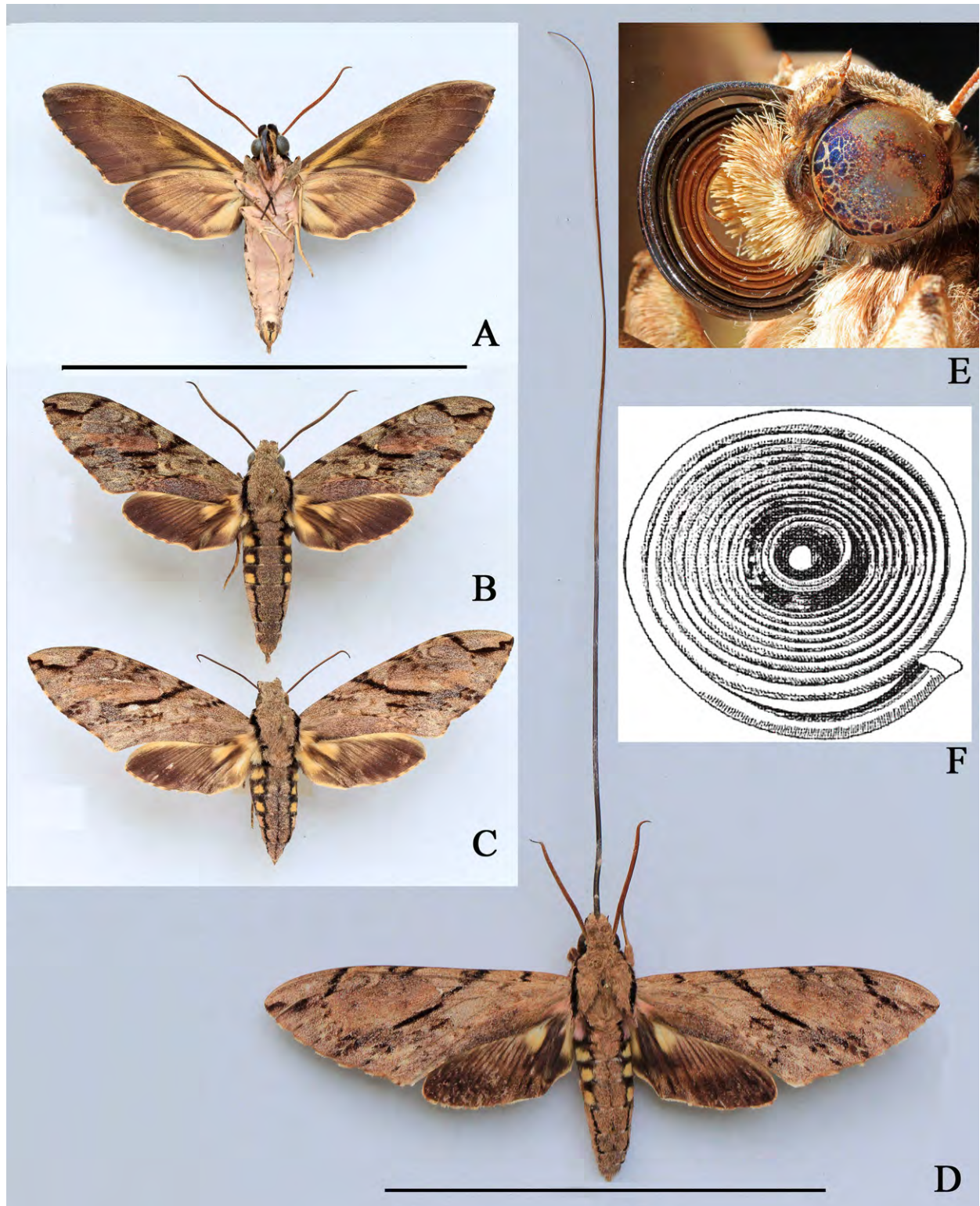


Figure 6. *Xanthopan morganii praedicta* from Madagascar. A, male of 5th generation bred in captivity, viewed from below. Underside of abdomen is pinkish whereas the underside of moths of the other subspecies from Africa (Fig. 7D, E) is white. B, same male viewed from above. Coloration, wing patterns and morphology are similar to moths from Gabon, Africa (Fig. 7). C, female of 5th generation bred in captivity. D, larger male from the wild. E, lateral view of head with proboscis and spiny labial palps of a male. Scale bars = 10 cm (L. T. Wasserthal). F, coiled long proboscis of a Brazilian moth (Müller, 1873).

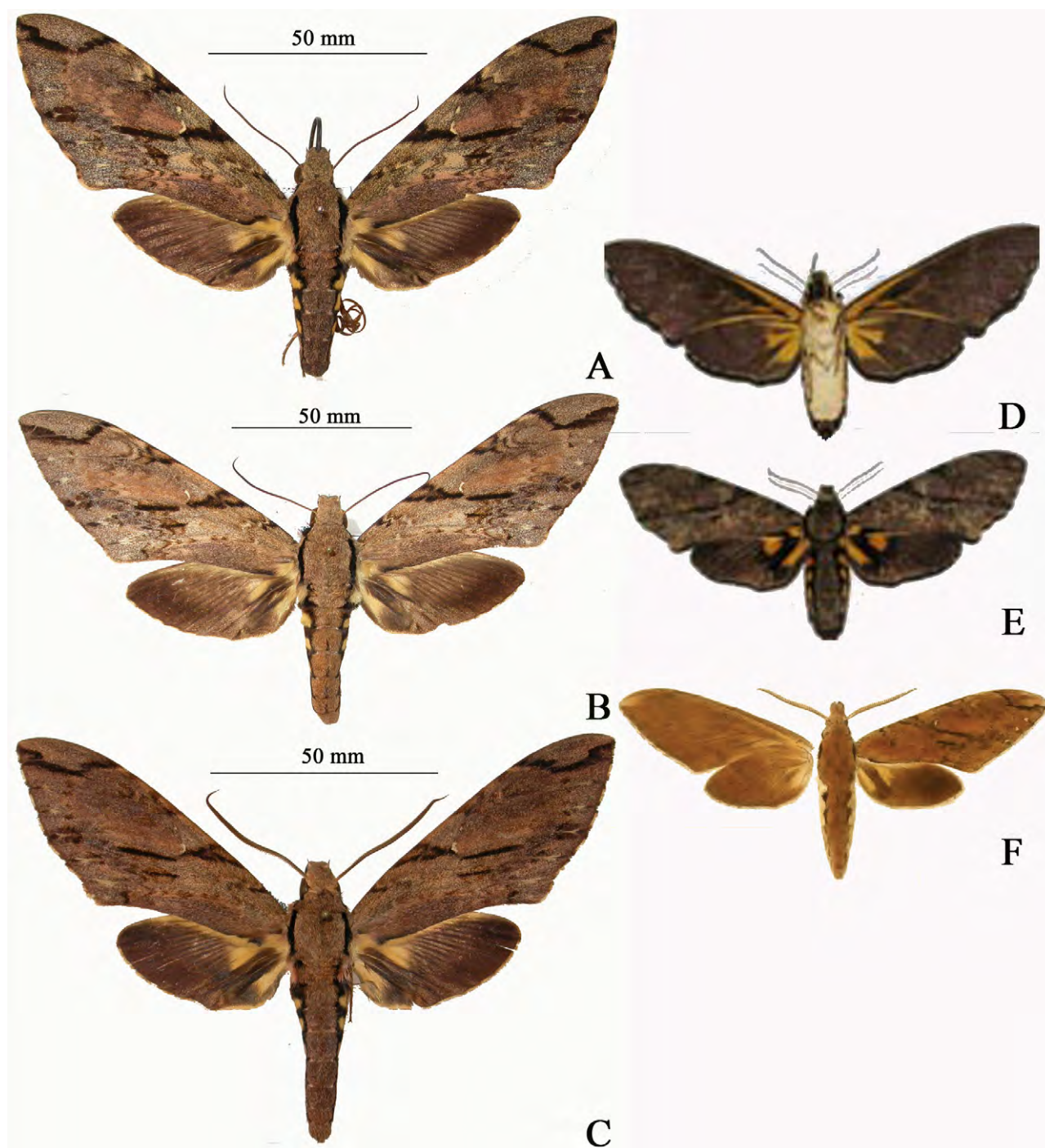


Figure 7. *Xanthopan* from Africa. A–C, three *Xanthopan morgani* moths from Gabon showing differences in body and wing size and coloration (courtesy Patrick Basquin, La Valette, France, and Rodolphe Rougerie from the Barcode of Life Datasystems, <http://www.boldsystems.org/views/login.php> with assistance from James Robertson). If the species *Xanthopan morgani* is variable at least to the extent seen here it is reasonable to assume that the same may be true for the subspecies *Xanthopan morgani praedicta*. D, *Xanthopan morgani morgani* from The Gambia viewed from below, wingspan 13.8 cm, body length in dry state 6 cm (courtesy Roy Goff). E, *Xanthopan morgani* from The Gambia, wingspan 13.8 cm, body length in dry state 6 cm (courtesy Roy Goff). F, *Xanthopan morgani praedicta* viewed from above, perhaps the first colour painting of this subspecies, right side viewed from above and left wing from below (Oberthür, 1920).

Table 4. Body size and proboscis length of *Xanthopan morgani* and *Xanthopan morgani praedicta*

Species	Wingspan or forewing length (cm)	Body length (cm)	Proboscis (cm)		Proboscis length/forewing length	Weight (g)		References, comments and/or additional information
			Length	Width		Male	Female	
<i>Xanthopan morgani</i>	12		19.5					Rothschild & Jordan (1903)
	10.9–13	4.2–4.6	>22					Pinhey (1962) R. Goff (pers. comm.) Walker (1856)
<i>Xanthopan morgani praedicta</i>			22.5					Rothschild & Jordan (1903)
			19.6 ± 2.8	0 = 0.73				Nilsson <i>et al.</i> (1985)
			18.8					Nilsson <i>et al.</i> (1987); Nilsson & Rabakonandrianina (1988)
			~25					Nilsson (1988)
			up to 25					Nilsson (1998a)
			14.7–24.4					Wasserthal (1997)
	7.7 ± 0.63	6.5 ± 0.70	22 (♂)					
			21.4 (♀)					
	7.3 (♂), 8.2 (♀)		21.7 ± 0.42		2.8 ± 0.28	1.9 ± 0.15	3.0 ± 0.31	young female* after laying 70 eggs† same old female‡
			22 (♂), 21.4 (♀)			1.7–2.9	4.36 2.64 1.96	Kritsky (2001) R. Goff (pers. comm.)
	15		~30					
	13.8	6.0						
	15 (♂)							
	16.4 (♀)							
			22					Denso (1943)
			>20					Micheneau <i>et al.</i> (2010)

*Prior to 7 September.
†After laying 70 eggs, 10 September.
‡One day before death, 24 September.

is in a less well known second letter Darwin wrote to Hooker 5 days later (Darwin, 1862c): 'Bateman has just sent me a lot of orchids with the *Angraecum sesquipedale* [this time he uses the correct name]: do you know its marvelous nectary 11½ inches [29.2 cm] long, with nectar only at the extremity. What a proboscis the moth that sucks it, must have! It is a very pretty case.' This second letter is important for two reasons. First, the fact that Darwin wrote two letters about *A. sesquipedale* within 5 days to the same recipient indicates that he was truly fascinated and excited by this orchid. Second, this is first time Darwin mentioned a moth. The idea that *A. sesquipedale* is pollinated by a moth may have occurred to him because of observations that pollinia of *Orchis* L. become attached to probosces of moths and his familiarity with English sphinxes (Darwin, 1904). These observations and the second letter to Hooker (1862c) probably led to what he wrote in *Contrivances*: 'in Madagascar there must be moths with probosces capable of extension to a length of between ten and eleven inches [25.4–27.9 cm]' (page 188 in the first edition, Darwin, 1862a and p. 163 in the second edition, Darwin, 1904) and 'in Madagascar *Angraecum sesquipedale* must depend on some gigantic moth' (p. 282 in the second edition, Darwin, 1904 – publication date was 1877).

Darwin died in 1882. His 'gigantic moth' was described 41, 26 and 21 years after the first and second editions and his death, respectively (Rothschild & Jordan, 1903) and named *X. morganii praedicta* [they actually used the orthography 'morganii'] for its predicted discovery. It is not certain whether the moth was named in honour of Darwin's prediction. In the original description of *X. morganii praedicta*, there is no mention of Darwin, only of Wallace's comments in *Natural Selection*. Therefore, it may be that it is this prediction that was honoured. Probably the most generous interpretation would be that the moth was named for its predicted discovery in general, rather than anyone's prediction in particular. Indeed, there is only a passing reference to Darwin in the introduction of the 'Revision' of Rothschild & Jordan (p. xli) where they referred to the 'Darwinian Revolution' and the *Origin* in their discussion of how barriers between species arose.

Collections which contained the male (Fig. 6A, B, D, E) and female (Fig. 6C) specimens were known at the time. However, the collector(s), location(s) and time(s) of collection(s), if known, were not published (Rothschild & Jordan, 1903). A romantic and dramatic story in an orchid hobbyist magazine about its discovery (Fowlie, 1969) is a contrived fable which bears no relation to the truth or reality. The proboscis of *X. morganii praedicta* is gigantically long (up to 15 cm; Fig. 6D; Table 4), but the moth itself

(Fig. 6A–D) is not gigantic. Its wingspan (up to 16 cm; Table 4) is only about half that of the truly gigantic *Attacus atlas* (up to 26 cm) and *Thysania agrippina* Cramer (up to 31 cm). *Xanthopan morganii morganii* is even smaller (Fig. 7A–C).

POLLINATOR

Until 1903, an unknown moth with a long proboscis, and after that *X. morganii praedicta*, was assumed to be the pollinator of *A. sesquipedale*. However, for most of this time no one actually recorded visits by the moth to *Angraecum* flowers in Madagascar (Denso, 1943–1944; van der Pijl & Dodson, 1966; Denso was a businessman, German consul in Karachi and naturalist who collected moths; the hawkmoth *Nephele densoi* was named for him by Wilhelm Moritz Keferstein in 1870).

In fact, such visits were not observed until 1992. The first evidence that *X. morganii praedicta* pollinates *A. sesquipedale* was obtained when a male moth bearing a viscidium of the orchid was captured in that year. Visits of *X. morganii praedicta* to *A. sesquipedale* and *A. compactum* Schltr. were recorded on tape in 1992 with night vision equipment to determine the effects of swing-hovering flight. The visits were also photographed in 1992 (130 years after Darwin's prediction; Wasserthal, 1993, 1996, 1997) and subsequently videographed in 2004 by Dr Philip J. DeVries of the University of New Orleans 143 years after Darwin postulated the mechanism of pollination (<http://www.youtube.com/watch?v=fwB5gDBgOYs> or <http://www.youtube.com/watch?v=OMVN1EWxfAU>). All descriptions, depictions (Figs 3A–E, 5A) and experiments (Fig. 3A–C, F, G) until then were based on conjecture and Darwin's experiments (Darwin, 1904).

On receiving the plants, Darwin wrote (Darwin, 1862a): 'A green, whip-like nectary of astonishing length hangs down beneath the labellum. In several flowers sent me by Mr. Bateman I found the nectaries eleven and a half inches [29.2 cm] long, with only the lower inch and a half [3.8 cm] filled with nectar. What can be the use, it may be asked, of a nectary of such disproportionate length? We shall, I think, see that the fertilisation of the plant depends on this length, and on nectar being contained only within the lower and attenuated extremity. It is, however, surprising that any insect should be able to reach the nectar . . . in Madagascar there must be moths with probosces capable of extension to a length of between ten or eleven inches [25.4–27.9 cm]! . . . I could not for some time understand how the pollinia [Figs 3I, 5D] of this orchid were removed, or how the stigma [Fig. 3C, H] was fertilised (Fig. 3G). I passed bristles and needles down the open entrance into the nectary and through the cleft in the rostellum with no results. It

then occurred to me that, from the length of the nectary, the flower must be visited by large moths, with a proboscis thick at the base [Fig. 3E, F, both based on conjecture]; and that to drain the last drop of nectar, even the largest moth would have to force its proboscis as far down as possible... the moth... would... be... forced to push its proboscis through the cleft... by slight pressure the whole foliaceous rostellum is depressed. The distance from the outside of the flower to the extremity of the nectary can thus be shortened by a quarter of an inch [6.35 mm]. I therefore took a cylindrical rod one-tenth of an inch [2.54 mm] and pushed it down through the cleft of the rostellum. The margins readily separated, and were pushed downwards together with the whole rostellum. When I slowly withdrew the cylinder the rostellum rose from its elasticity, and the margins of the cleft were upturned so as to clasp the cylinder. Thus the viscid strips of membrane on each underside of the cleft rostellum [Fig. 3C, G, H] came into contact with the cylinder, and firmly adhered to it; and the pollen-masses were withdrawn [J.A. and his graduate student in the early 1970s, Dr Michael S. Strauss, tried this with a teasing needle and had the same result; Fig. 3F]. By this means I succeeded every time in withdrawing the pollinia; and it cannot, I think, be doubted that a large moth would thus act [as in Fig. 3E, a conjecture drawn in the 1960s in Singapore]; that is, it would drive its proboscis up to the very base through the cleft of the rostellum so as to reach the extremity of the nectary; and then the pollinia attached to the base of the proboscis would be safely withdrawn.'

'I did not succeed in leaving the pollen masses on the stigma so well as I did in withdrawing them... when a moth with the pollinia adhering to the base of its proboscis, inserts it for a second time into the nectary, and exerts all its force so as to push down the rostellum as far as possible, the pollen-masses will generally rest on and adhere to the narrow, ledge-like stigma which projects beneath the rostellum [Figs 3C, G, 5B]. By acting in this manner with the pollinia attached to a cylindrical object, the pollen masses were twice torn off and left glued to the stigmatic surface [Dr Strauss and I managed to deposit pollinia which were attached to a teasing needle, but they became attached to the rostellum without touching the stigma; Fig. 3G].'

As already mentioned, visits by *X. morganii praedicta* to *A. sesquipedale* were not observed (van der Pijl & Dodson, 1966) until 1992 when several papers and a number of photographs (Figs 8B, D, 10A–D; Wasserthal, 1993, 1996, 1997) were published showing *A. sesquipedale* being pollinated by *X. morganii praedicta* on rocky coastal slopes north of Fort Dauphin in south-eastern Madagascar during August

1992. The behaviour of captured *X. morganii praedicta* was observed in textile gauze tents measuring 3.6 m × 3.6 m × 2.5 m (height) at the same site. Additional studies using captured and reared moths were carried out in greenhouses at the University of Erlangen, Germany, from 1992 until 1996 (Wasserthal, 1997). Extensive observations in Madagascar, which showed that few flowers set fruit, were taken as an indication that 'there was no chance of observing a pollinator on *A. sesquipedale* [in the wild of that area]. Therefore moths were captured and confronted with virgin flowers under optimal conditions in a large flight tent' (Wasserthal, 1997: 344, 346).

PREDATORS

Before proceeding with descriptions of visits to *A. sesquipedale* by *X. morganii praedicta* it is necessary to describe a tripartite coevolution between orchids, their pollinators and predators which prey on the latter. In Colombia a camouflaged *Epicadus heterogaster* spider (Fig. 9Aa, arrow, 9Ad) on *Cynoches chlorochilon* Klotsch. (Fig. 9Aa, Ab) which had captured the pollinator, *Euglossa fasciata* (Fig. 9Aa, wedge, 9Ac) was described as an 'anti-pollinator' (Ospina, 1969). Another 'anti-pollinator' in Colombia (Ospina, 1969) is a white spider which mimics part of the labellum of *Epidendrum ciliare* L. (Fig. 9Ca, Cb) so perfectly that it is nearly invisible (Fig. 9Cb, arrow, 9Cc, arrow). A more sinister 'anti-pollinator' is the snake *Bothrops atrox* (Fig. 9Bd), which lurks near the yellow flowers of *Elleanthus xanthocomus* Rchb.f. (Fig. 9Ba, Bc) and preys on visiting hummingbirds (Fig. 9Bb) which visit them (Ospina, 1969).

Dendrobium crumenatum Sw. produces numerous fragrant ephemeral flowers synchronously and gregariously 9 days after a rain (see Arditti, 1989 for a review). Pollinating bees (Fig. 9E) hover among the flowers and visit them. Spiders weave webs in front of the flowers and catch some of the bees (observed by the late Dr Djunaïdi Gandawijaja and J.A. at the Bogor Botanical Gardens, Indonesia, in the early 1970s). Spider webs can also be seen around flowers of *Ceratochilus biglandulosus* Blume (Comber, 1990; Fig. 9D). In Canada a crab spider has been photographed on *Pogonia ophioglossoides* (L.) Juss. (Fig. 9F).

Predatory spiders approximately 2 cm long of the family Sparassidae lurk among flowers in Madagascar and prey on the pollinators (Fig. 8A, C; Wasserthal, 1996). To avoid being caught the moths swing from side to side in what has been described as a pendular hover (Wasserthal, 1993, 1996) or 'swing-hovering'. The frequency of this hovering is 1–2 Hz at angles which range from 25° to almost 360° (Fig. 8E; Wasserthal, 1996).



Figure 8. Pollinators, pollination, flowers and predators. A, *Panogena* moth feeding in the presence of a spider which is presumably stalking it. B, *Xanthopan morganii praedicta* pollinating *Angraecum sesquipedale* (Wasserthal, 1997). This photograph appeared on the cover of *Botanica Acta* (successor to *Berichte der Deutsche Botanische Gesellschaft*) volume 110, number 5. C, *Coelonia brevis* hawkmoth in the grasp of a spider which caught it in midair (Wasserthal, 1996). D, *Xanthopan morganii praedicta* on approach flight to a flower of *Angraecum sesquipedale* (Wasserthal, 1996). A viscidium which is visible at the base of the proboscis was the first documentation of a successful visit of *Xanthopan morganii praedicta* to *Angraecum sesquipedale*. The bright spot on the proboscis is nectar, which indicates that the moth previously inserted its proboscis into the nectary to depth of at least 14 cm. E, stroboscopic photograph of a convolvulus hawkmoth (*Agrius convolvuli*) sucking nectar from a composite inflorescence while swing-hovering (Wasserthal, 1996). *Xanthopan morganii praedicta* behaves in a similar manner while visiting flowers of *Angraecum sesquipedale* (Wasserthal, 1997).



Figure 9. Predation on orchid pollinators. A, a, *Epicadus heterogaster* spider (arrow) on *Cynoches chlorochilon* flower and a *Euglossa* bee (wedge) it has caught. B, *Cynoches chlorochilon* flower. C, *Euglossa* bee. D, *Epicadus* spider (Ospina, 1969; Joseph Arditti's laboratory; Wikipedia/Wikimedia). B, a pit viper, the fer-de-lance, *Bothrops atrox* (d) lurks around flowering plants of *Elleanthus xanthocomus* (a, c) to catch the humming-birds (b) which pollinate it (Ospina, 1969; Wikipedia/Wikimedia). C, spider (arrows in a and enlarged in c) lurk on labella of *Epidendrum ciliare* (a, b) to prey on pollinators (Ospina, 1969; Joseph Arditti's laboratory). D, *Ceratochilus biglandulosus* surrounded by spider webs which are intended to catch pollinators (the late James Comber; see Comber, 1990 for details about this orchid). E, *Dendrobium crumenatum* with pollen-bearing pollinator (courtesy Greg Alikas, American Orchid Society). This orchid flowers gregariously in Indonesia, Malaysia and Singapore 9 days after a rainstorm producing numerous ephemeral pleasantly scented white flowers which attract many bees. Spiders build webs in front of the flowers and catch pollinators. F, crab spider lurking on rose *Pogonia* in Canada (courtesy John Neufeld).

Hunting spiders were already in existence when moths arose and started to evolve in response to them (Wasserthal, 2009). Therefore, it has been suggested that the long proboscises and swing-hovering (Fig. 8E) evolved as a predator avoidance mechanism (Wasserthal, 2009). This suggestion is based on confrontation experiments which show that long proboscises and swing-hovering prevent efficient predation (Wasserthal, 2009). Thus, it may be that long-spurred orchids such as *A. sesquipedale* benefitted from the pre-existence of moths which had proboscises that could pick up and transfer their pollinaria (Wasserthal, 2009). This co-opting view modifies Darwin's suggestion (Wasserthal, 1997) that the long proboscises of tropical hawkmoths such as *X. morganii praedicta* evolved in a coevolutionary race between long spurs (i.e. nectar tubes) and tongues (Wasserthal, 2009; also see below).

XANTHOPAN MORGANII PRAEDICTA VISITS TO *ANGRAECUM SESQUIPEDALE*

To study visits of *X. morganii praedicta* to *A. sesquipedale*, a captured virgin female moth exposed to flowers during August and September in a large flight cage (Wasserthal, 1997) 'was uninterested in visiting flowers but primarily rested in an alluring position. After copulation with [a captured] male, it began searching for flowers. The female visited two *A. sesquipedale* flowers on August 29, while the male visited two on August 28 and three more on August 30' (Wasserthal, 1997: 346). A viscidium of *A. sesquipedale* which must have been attached prior to the capture was present on the proboscis of the male (Fig. 10D).

Tongue insertion by the male and female moths into the spur of *A. sesquipedale* was rapid, lasted 1.00 ± 0.16 s and did not involve swing-hovering (Wasserthal, 1997). 'Both hawkmoths seized the protruding labellum of the flower and pressed their heads as closely as possible towards the rostellum and rested $6 \text{ s} \pm 0.84$, shivering scarcely or not at all [Fig. 10A]. They approached the flower from below [Fig. 8B] and withdrew the tongue flying backward and upward [Fig. 10B; this can also be seen in videos by Wasserthal and DeVries]. This lasted $0.90 \text{ s} \pm 0.45$. In all cases pollinaria were removed from the flower and attached to the moths' tongues 4–9 mm distant from their base [Fig. 10B, C, F]. Some seconds later, the pollinaria stalks bent aside at a right angle from their initial orientation parallel to the tongue axis [Fig. 10C]. During the following visits, the pollinaria were deposited. When entering a new flower from below, the tongue with the pollinia passed unhindered through the wide opening of the spur mouth. During withdrawal, the tongue was guided by the dorsal slit

in the rostellum and the laterally exposed pollinia were transferred to the sticky surfaces of the stigma. The removal and the deposition of the pollinaria took place when the moth was in leg contact with the labellum. The last pair of non-deposited pollinaria at the tongue base of the female remained undamaged from August 29 to September 21 when the moth died . . .' (Wasserthal, 1997: 346).

When visiting artificial flowers and those of *Clerodendron* L. and *Lantana* L. (Verbenaceae) male and female *X. morganii praedicta* exhibited swing-hovering (Wasserthal, 1997). Swing-hovering is normally spontaneous and needs no induction by external stimuli. Most male and female *X. morganii praedicta* exhibited swing-hovering spontaneously (16 of 19 individuals; Wasserthal, 1993). However, swing-hovering could be elicited by mechanical means, such as gentle touching, in the minority of individuals (three of 19) which did not exhibit it spontaneously (Wasserthal, 1993). Hampering of tongue retraction has also been observed to act as a stimulus for swinging flight. This happens when the spur of a flower is narrow and presumably causes strong friction.

Swing-hovering moths stop swinging when they seize the protruding labellum of *A. sesquipedale*. This is a precondition for a successful transfer of pollinaria. Swing-hovering generally starts after contact of the tip of the proboscis with the nectary. Only stressed moths were already swinging when their proboscis touched the labellum.

Regardless of whether they swing-hover or not, *X. morganii praedicta* males and females visit *A. sesquipedale* flowers for nectar. No nectar was present in five out of 20 flowers (Wasserthal, 1997). Nectar content in the other 15 varied from 40 to 300 μL with levels in the spurs ranging from 7 to 25 cm (Wasserthal, 1997; Fig. 11A, B, E; Table 2). Flowers with the longest spurs contained the largest volume (Fig. 11A). The correlation between volume and spur length (Fig. 11A) and mean nectar volume ($165 \pm 89.91 \mu\text{L}$) and average column height (16.9 ± 5.98 cm; Fig. 11B, E) suggests that nectar column height may reach a minimal distance from the opening regardless of spur length. Among the flowers studied the height of the nectar column was always such that an *X. morganii praedicta* with an average proboscis length (22 cm) could reach it (Fig. 11E; Tables 2, 4; Wasserthal, 1997). Such moths can obtain 50 μL per visit with 70% of the nectar remaining out of their reach (Wasserthal, 1997). Thus, an *X. morganii praedicta* requiring 400–1000 μL per night would have to visit 8–20 flowers and fly for a maximum of 50 min (Wasserthal, 1997). Visits by *X. morganii praedicta* to *A. sesquipedale* flowers last 0–7 s (Fig. 11D; Wasserthal, 1997).

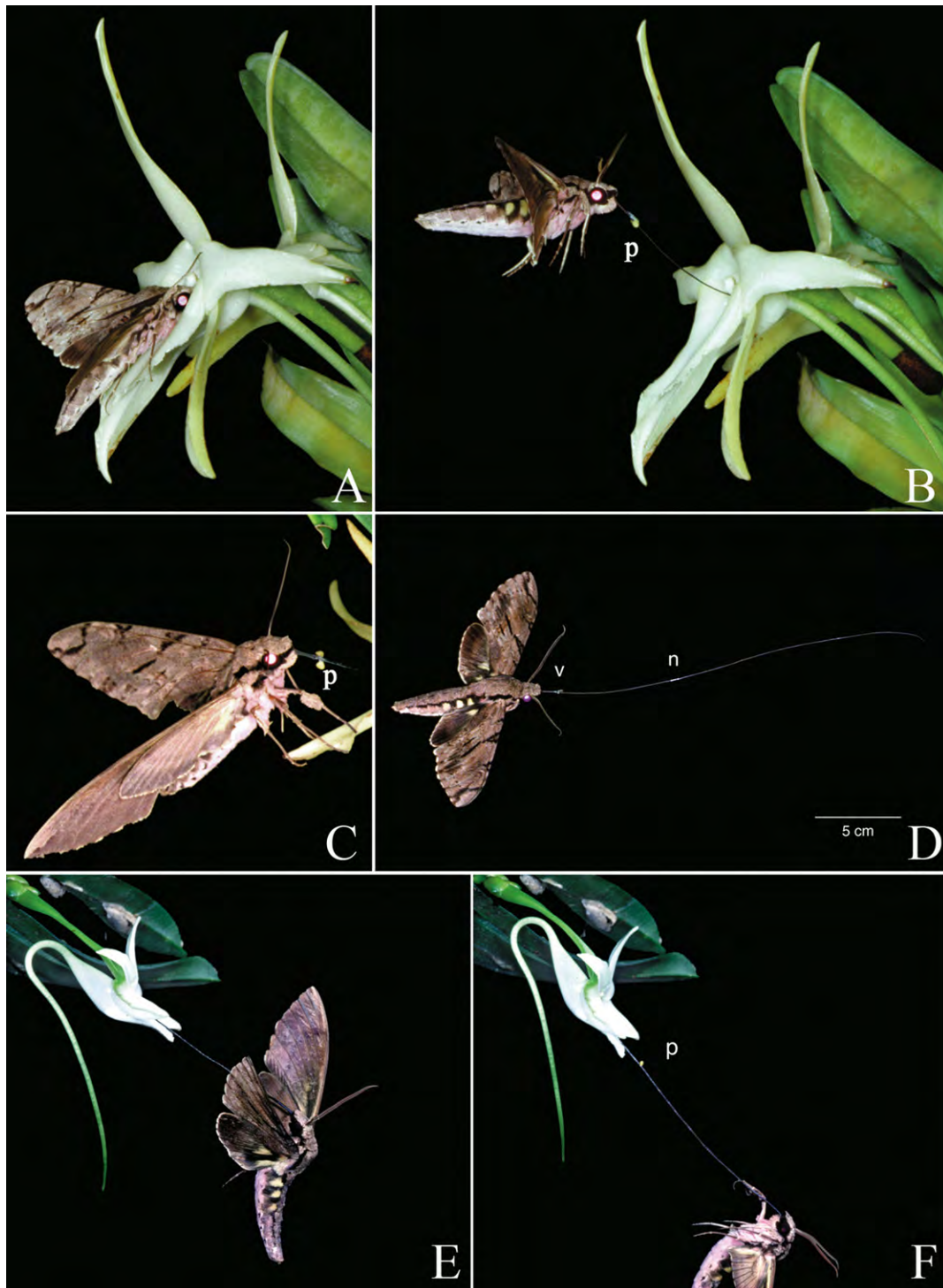


Figure 10. *Xanthopan morgani praedicta* visiting flowers of *Angraecum sesquipedale* (A–D) and *Angraecum compactum* (E, F). A, male moth positioned on the labellum during a visit. B, visiting moth flying up as it withdraws its proboscis which has a pollinarium (p) attached to near the base of its proboscis. The pollinia lie flat against the proboscis because their stipes are parallel to it. C, female moth with laterally positioned pollinia on the tip of a labellum. D, a male moth flying in an enclosure immediately after its capture. The tongue bears a viscidium (v) near its base and a remnant (n) of what is probably nectar 7.9 cm from the base. E, maximal insertion of proboscis just before the start of withdrawal. F, pollinaria (p) are removed during withdrawal (A–F, Wasserthal, 1997). Pollinia of *Angraecum sesquipedale* are transferred. Those of *Angraecum compactum* are not (Wasserthal, 1997).

COEVOLUTION

In the second edition of *Contrivances* Darwin referred to a nectary of ‘astonishing length’ exceeding 11 inches, and a ‘gigantic moth’ with a ‘wonderfully long proboscis’ which withdraws the pollinia while trying to drain the last drop of nectar (Darwin, 1904).

THE MOTH

Darwin was right about the length of the proboscis, but not regarding the size of the moth. *Xanthopan morgani* (Fig. 7A–C) and *X. morgani praedicta* (Figs 6A–9D, 7D, E) are not small but nor are they ‘gigantic’ or ‘huge’. However, this does not really matter because only the proboscis must be long enough, and *X. morgani praedicta* is certainly large, heavy and powerful enough (Table 4) to exert the force necessary to insert its long proboscis deeply enough, pick up the pollinaria on withdrawing it (Fig. 10B–D) and deposit them on a subsequent visit to another flower (as in the simulation in Fig. 3F, G).

Referring to the flowers sent to him by Bateman, Darwin wrote: ‘If the *Angraecum* in its native forests secretes more nectar than did the vigorous plants sent me . . . so that nectary . . . becomes filled, small moths might obtain their share, but they would not benefit the plant. The pollinia would not be withdrawn until ‘some huge moth, with a wonderfully long proboscis, tried to drain the last drop of nectar. If such great moths were to become extinct . . . the *Angraecum* would become extinct. On the other hand, as the nectar, at least in the lower part of the nectary, is stored safe from . . . other insects, the extinction of the *Angraecum* would probably be a serious loss to these moths. We can thus understand how the astonishing length of the nectary had been acquired by successive modifications. As certain moths in Madagascar became larger through natural selection . . . , or as the proboscis alone was lengthened to obtain honey from . . . *Angraecum* and other deep tubular flowers, those individual plants of the *Angraecum* which had the longest nectaries . . . and . . . compelled the moths to insert their proboscides up to the very base, would be best fertilised. These plants would yield most seeds, and the seedlings would generally inherit long nectaries; and so it would be in successive generations of the plant and of the moth. Thus, it would appear that there has been a race in gaining length between the nectary of the *Angraecum* and the proboscis of certain moths; but the *Angraecum* has triumphed . . .’ (Darwin, 1904: 165).

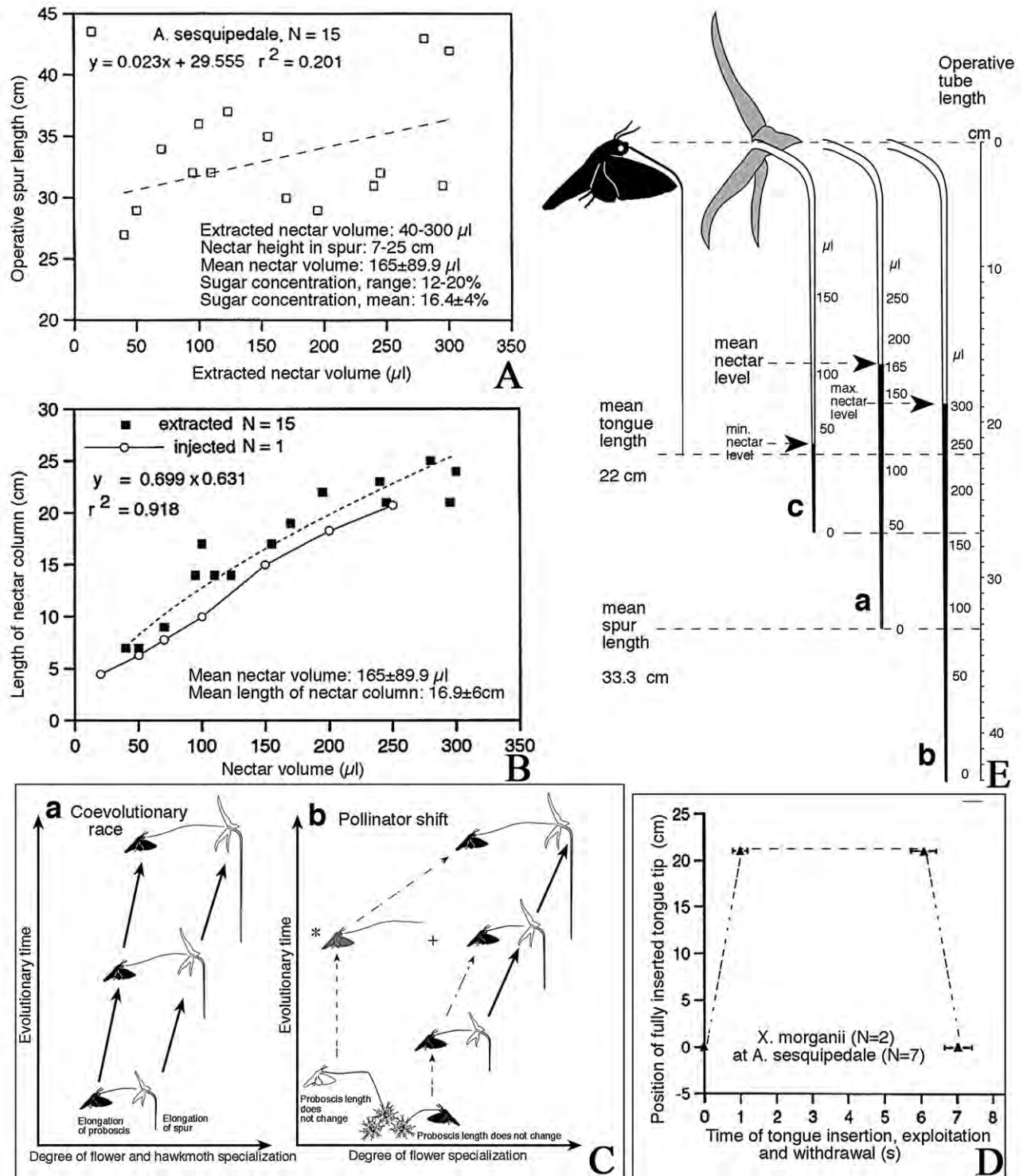
CRITICISM AND REBUTTAL

Campbell questioned the passage above basing his criticism on Darwin’s statement the ‘We can thus

partially [emphasis by Campbell] understand how the astonishing length of the nectary may have been acquired by successive modifications’ (Campbell, 1884). Campbell’s contention was that Darwin’s ‘explanations of the mechanical methods by which a wonderful *Orchis* is pollinated [here the word “*Orchis*” seems to mean “orchid”] are indeed, as he himself says, with great candor “partial” and partial only. How different from the clearness and the certainty with which Mr. Darwin is able to explain to us the use of intention of the various organs! . . . We know, too, that these purposes and ideas are not our own, but . . .’ a creator (Campbell does not use the word, but implies it).

Darwin did indeed refer to or imply intentions and purposes, but he always spoke of them as the consequences of natural selection and the means, which shape design, not as theological teleological tendencies (Lennox, 1993) and certainly not as ‘the Living Will [of] . . . a Personal God’ Campbell wanted to inject into science and which is the main basis for his criticism, polite and carefully worded as it was (Campbell, 1884). Darwin did not reply to Campbell. However, Wallace did and indicated to Darwin that he ‘shall be glad to know whether I have done it right by you, and hope you will not be so very sparing of criticism as you usually are’ (Wallace, 1867b). Wallace’s reply to Campbell started with a pointed, long, but well-constructed sentence: ‘The noble author represents the feelings and expresses the ideas of that large class who take a keen interest in the progress of Science in general, and especially that of Natural History, but have never themselves studied nature in detail, or acquired that personal knowledge of the structure of closely allied forms – the wonderful gradations from species to species and from group to group, and the infinite variety of the phenomena of “variation” in organic beings, – which are absolutely necessary for a full appreciation of the facts and reasoning contained in Mr. Darwin’s great work’ (Wallace, 1867a).

Wallace then elaborated on Darwin’s suggestion regarding the origin of long nectary and proboscises: ‘Now let us start from the time when the nectary was only half its present length or about six inches, and was chiefly fertilized by a species of moth which appeared at the time of the plant’s flowering, and whose proboscis was of the same length. Among the millions of flowers of the *Angraecum* produced every year some would always be shorter than the average, some longer. The former, owing to the structure of the flower, would not get fertilized, because the moths could get all the nectar without forcing their trunks down to the very base. The latter would be well fertilized, and the longest would on the average be best fertilized of all. By this process alone the average



length of the nectary would annually increase, because the short ones being sterile and the long ones having abundant offspring, exactly the same effect would be produced as if a gardener destroyed the short ones and sowed the seed of the long ones only;

and this we know by experience would produce a regular increase of length, since it is this very process which has increased the size and changed the form of our cultivated fruits and flowers. But this would lead in time to such an increased length of the nectary

Figure 11. Nectar: sugar content and height of column, proboscis length and coevolution. A, correlation between spur length and extracted nectar volume (modified from Wasserthal, 1997 by the removal of data about species other than *Angraecum sesquipedale* and the addition of the five lines of text at the base of the figure). B, correlation between height of nectar column and nectar volume measured by extraction and injection (modified from Wasserthal, 1997 by the addition of the two lines of text which start with 'Mean'). C, comparison between Darwin's 'coevolution race' and Wasserthal's 'pollinator shift' models. In the 'coevolution race' model (A) the race is between increasing lengths of spurs and proboscises. The 'pollination shift' model (B) involves the recruitment by long-spurred angraecoid orchids of pollinators which are generalist feeders and have proboscises of different lengths. These pollinators are substituted gradually. When spurs enlarge beyond a certain length due to evolutionary pressure by the primary visitors flowers can be exploited (i.e. nectar can be taken from them) by illegitimate visitors with longer proboscises (*). This has been observed in interactions between *Xanthopan morgani praedicta* and *Coelonia solani* with *Angraecum compactum*. Increased selective pressure is exerted by the existence of moth species with long proboscises. Flowers become deceptive, but can still be pollinated when spurs become too long for the primary pollinator to reach the nectar. Pollination is impossible when the proboscis is longer than the spurs because the pollinaria are attached further from the base of the proboscis. When this happens the pollinaria are scratched away by the forelegs when the proboscis is rolled to a loose spiral. If the proboscis is shorter than the spur, transfer of the pollinaria is possible as long as the proboscis can get in contact with the sexual organs of the orchid. This occurs in other angreoid orchids. Explanation of symbols: *, illegitimate visitor with a long proboscis which exploits flowers; black moth, orchid pollinator; grey moth, non-pollinating visitor; white moth, a moth incapable of pollinating an orchid (modified from Wasserthal, 1997 by moving and adding labels). D, correlation between position of fully inserted proboscis and time of insertion, stay and withdrawal (modified from Wasserthal, 1997 by the removal of data not pertaining to *Angraecum sesquipedale*). E, Nectar accessibility in *Angraecum sesquipedale* spurs. a, moth with an average spur length of 22 cm can obtain about 50 µL nectar from a spur of average length of 33.3 cm and an average nectar volume of 165 µL. b, a spur 43 cm long could offer nectar to a moth with a 22-cm-long proboscis only if it contains more than 240 µL solution. C, small volumes of nectar can be exploited if the spur is 27 cm long (Wasserthal, 1997).

that many of the moths could only just reach the surface of the nectar, and only a few with exceptionally long trunks be able to suck up a considerable portion. This would cause many moths to neglect these flowers because they could not get a satisfying supply of nectar, and if these were the only moths in the country . . . further growth of the nectary [would] be checked . . . But there are . . . moths of various lengths of proboscis, and as the nectary became longer . . . larger species would become the fertilizers . . . till the largest moths became the sole agents . . . the moths would also be affected, for those with the longest probosces would get most food, would be the strongest and most vigorous, would visit and fertilize the greatest number of flowers and would leave the largest number of descendants. The flowers . . . fertilized by these moths being those which had the longest nectaries, there would in each generation be on the average an increase in the length of the nectaries, and also an average increase in the length of the proboscis of the moths, and this would be a *necessary result* [emphasis in the original] from the fact that nature ever fluctuates about a mean . . .' (Wallace, 1867b). A recent report that spurs of *Satyrium longicauda* can vary in length from 13 to 46 mm (van der Niet, Liltved & Johnson, 2011) substantiates Wallace's assumption that some spurs will be shorter and others longer.

Darwin's ideas and Wallace's logic (Fig. 5A) are still being considered (Nilsson *et al.*, 1985, 1987; Nilsson,

1988, 1992; Nilsson & Rabakonandrianina, 1988; Kritsky, 2001; Johnson & Edwards, 2000; Micheneau *et al.*, 2008, 2010; Hoot, 2009; Kutschera & Briggs, 2009). However, Campbell's contention that there is 'no shyness [in] illustrating Divine things by reference to the Natural', if it is even remembered by more than a few, is of interest only to those who seek and/or believe in pre-existing 'Purpose and Design' (Campbell, 1884) in nature, rather than relying on science and evolution.

COEVOLUTIONARY RACE VS. POLLINATOR-SHIFT

The pollination of *A. sesquipedale* by *X. morgani praedicta* is the best known instance of a fit between a proboscis or tongue length and that of an orchid spur or nectary. Less well known instances are those of the orchids *Platanthera ciliaris* (L.) Lind. and the butterflies *Papilio troilus* and *Papilio palamedes* in the south-eastern United States (Robertson & Wyatt, 1990) and *Disa draconis* Sw. (*sensu* Linder 1981) and the horsefly *Philoliche rostrata* and the tanglewing fly *Moegistorhynchus longirostris* in South Africa (Johnson & Steiner, 1997). All three (*Angraecum*–*Xanthopan*, *Platanthera*–*Papilio* and *Disa*–*Moegistorhynchus*) are examples of directional evolutionary trends (Whittall & Hodges, 2007) toward long spurs (Micheneau *et al.*, 2010). These traits evolved as a result of the interactions between the orchid and its pollinator (Whittall & Hodges, 2007; Micheneau *et al.*, 2010). Two hypotheses, described as

competing (Micheneau *et al.*, 2010), have been advanced to explain the evolution of long floral spurs. Darwin's coevolutionary race concept (Darwin, 1862a) attributes the elongation of spurs and proboscises to increases over time due to increased reproduction efficiency for the orchid and more efficient nectar foraging by the insect (Whittall & Hodges, 2007; Micheneau *et al.*, 2010).

A more recently advanced sequential (or co-opting) coevolution hypothesis (Wasserthal, 1997) which challenges Darwin's idea of coevolution is based on the concept that both the long proboscises and swing-hovering evolved as a predator avoidance mechanism and *A. sesquipedale* benefited from moths with these pre-existing traits because they could pick up and transfer pollinaria as their proboscises were long enough (Wasserthal, 2009). According to this hypothesis what occurred was a pollination shift by the plant to *X. morganii praedicta* and one-sided plant adaptive evolution; hence it is referred to as the pollinator-shift hypothesis (Wasserthal, 1996, 1997, 1998, 2009; Nilsson, 1998a; Svensson, Rydell & Töve, 1998; Jermy, 1999).

Criticisms of the pollinator-shift hypothesis are that: (1) evidence for predator avoidance is not unequivocal, (2) there are no quantitative data reports of consistent ambushing of large hawkmoths, (3) only smaller hawkmoths are sometimes captured by single large spiders or mantids and (4) due to the large size of the long-tongued hawkmoth guild in Madagascar it is more likely for the long tongue of *X. morganii praedicta* to have originated in a 'coevolutionary race between hawkmoths competing for nectar' (Nilsson, 1998a). These criticisms generated a discussion (Nilsson, 1998b; Samways, 1998; Svensson *et al.*, 1998; Wasserthal, 1998) which was resolved in favour of the pollinator-shift hypothesis (Jermy, 1999).

CODA

Darwin first proposed the existence of a moth with a very long tongue which pollinates *A. sesquipedale* in 1862 (Darwin, 1862b, c). Such a moth was not known at the time and Darwin wrote that he was ridiculed by some entomologists for suggesting it. Wallace (1867a, b), the brothers Fritz and Hermann Müller (Müller, 1873, 1883; in Brazil and Germany, respectively) and Forbes (Beddard, 1885) supported Darwin's suggestion. Fritz Müller even sent his brother a coiled proboscis of a Brazilian moth (Fig. 6F) which although long was not of sufficient length to pollinate an orchid with a spur like the one of *A. sesquipedale*. Hermann Müller published an illustration of the proboscis (Müller, 1873; Fig. 6F). The moth which pollinates *A. sesquipedale*, *X. morganii praedicta*, was finally described 41 years later (Rothschild & Jordan,

1903), but it was not observed to pollinate *A. sesquipedale* then or even later (Denso, 1943). However, such was Darwin's authority and the force and logic of natural selection that it was assumed that *X. morganii praedicta* or a moth like it did pollinate *A. sesquipedale*. Reasonably accurate drawings were made on the basis of this assumption (Wallace, 1867a; Figs 4D, E, 6A). Actual visits of *X. morganii praedicta* to *A. sesquipedale* and removal of pollinia (Figs 8, 10) were finally reported 134 and 135 years after Darwin (Wasserthal, 1996, 1997). These reports were followed by a video in 2004 by Dr Philip DeVries of the University of New Orleans of a visit by *X. morganii praedicta* to *A. sesquipedale*.

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REFERENCES

- Anonymous.** 1857. *Angraecum sesquipedale*. *Gardeners' Chronicle* [No volume number]: 253 (probably by John Lindley, the editor at the time).
- Anonymous.** 1859. *Angraecum sesquipedale*. *Curtis's Botanical Magazine* **89**: t. 5113 (probably by W. J. Hooker).
- Anonymous.** 1862a. New books. *Journal of Horticulture, Cottage Gardener and Country Gentleman* N. S. 3 (28 old series): 163.

- Anonymous. 1862b.** Fertilization of orchids. *The London Review*. 14 June 1862: 553–554 (written by M. J. Berkely; see Hooker, 1862c).
- Anonymous. 1862c.** The various contrivances by which British and foreign orchids are fertilised by insects and on the good effects of intercrossing. By Charles Darwin, M. A. With illustrations. (Murray). *The Athenaeum* No. 1804, May 24, 1862: 683–685.
- Anonymous. 1862d.** Mr. Darwin's orchids. *The Saturday Review*. 18 October 1862: 486.
- Anonymous. 1862e.** Fertilization of orchids. By Charles Darwin. Murray. *The Parthenon* No. 6, 7 June 1862: 177–178.
- Anonymous. 1866.** *Angraecum sesquipedale*. *Gardeners' Chronicle* [No volume number]: 52 (probably by M. T. Masters, the editor at the time).
- Anonymous. 1883.** The late M. W. A. Forbes. *Nature* **28**: 12.
- Anonymous. No Date.** *Angraecum sesquipedale*. Downloaded and read in April–May 2011. Available at: <http://en.wikipedia.org/wiki/Angraecumsesquipedale>
- Arditti J. 1989.** History of several important orchid research contributions from south east Asia. *Malayan Orchid Review* (Singapore) **23**: 64–80.
- Arditti J. 1992.** *Fundamentals of orchid biology*. New York: Wiley.
- Babington CC. 1862.** Letter 3566-Babington, C. C. to Darwin, C. R., 22 May 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/darwinletters/calendar/entry-3566>
- Bateman J. 1862a.** Letter 3356-Bateman, James to Darwin, C. R. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3356>
- Bateman R. 1862b.** Letter 3357-Bateman, Robert to Darwin, C. R. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3357>
- Beatty J. 2006.** Chance variation: Darwin on orchids. *Philosophy of Science* **73**: 629–641.
- Beddard PE. 1885.** *The collected scientific papers of William Alexander Forbes*. London: M. A. E. H. Porter.
- Belt T. 1874.** *The naturalist in Nicaragua*. London: John Murray.
- Bentham G. 1862.** Letter 3554-Bentham, George to Darwin, C. R., 15 May 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3554>
- Bosser J, Morat P. 1972.** Contribution a l'étude des *Orchidaceae* de Madagascar. XVIII. *Adansonia* **12**: 73–78.
- Burmeister CHK. 1856.** Systematische Uebersicht der Sphingidae brasiliens. *Abhandlungen der Naturforschender Gesellschaft zu Halle* **3**: 298. (or 58)–314 (or 74). Burmeister also published in 1856 a monograph/book with the same title. The publisher was H. W. Schmidt in Halle, Germany. Available at: http://agricola.nal.usda.gov/cgi-bin/Pwebrecon.cgi?Search_Arg=CAT11027077&DB=local&CNT=25&Search_Code=GKEY&STARTDB=NALDB
- Butler AG. 1876.** Revision of the heterocerous Lepidoptera of the family Sphingidae. *Transactions of the Zoological Society of London* **9**: 511–644.
- Campbell GJD. (8th Duke of Argyll). 1884.** *Reign of law*. New York: A. L. Burt.
- Comber JB. 1990.** *Orchids of Java*. Kew: Bentham-Moxon Trust. Royal Botanic Gardens.
- Cribb P, Tibbs M. 2004.** *A very Victorian passion The orchid paintings of John Day 1863 to 1888*. Kew: Blacker Publishing & The Royal Botanic Gardens, Kew in Association with Thames & Hudson.
- Crüger H. 1863a.** Letter 4008-Crüger, Hermann to Darwin, C. R. 23 Feb 1863. Downloaded and read June–July 2011. Available at: <http://www.darwinproject.ac.uk/entry-4008>
- Crüger H. 1863b.** Letter 4124-Crüger, Hermann to Darwin, C. R. 23 Apr 1863. Downloaded and read June–July 2011. Available at: <http://www.darwinproject.ac.uk/entry-4124>
- Crüger H. 1863c.** Letter 4265-Crüger, Hermann to Darwin, C. R. 8 Aug 1863. Downloaded and read June–July 2011. Available at: <http://www.darwinproject.ac.uk/entry-4265>
- Crüger H. 1864.** A few notes on the fecundation of orchids and their morphology. *Botanical Journal of the Linnean Society of London* **8**: 127–135. plate 9.
- Darwin CR. 1862a.** *The various contrivances by which British and foreign orchids are fertilised by insects and on the good effects of intercrossing*. London: John Murray.
- Darwin CR. 1862b.** Letter 3411-Darwin, C. R., to Hooker, J. D., 25 January 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3411>
- Darwin CR. 1862c.** Letter 3421-Darwin, C. R., to Hooker, J. D., 30 January 1862. Downloaded and read August 2011. Available at: <http://www.darwinproject.ac.uk/entry-3421>
- Darwin CR. 1862d.** Letter 3609-Darwin, C. R., to Murray, J., 18 [June 1862]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3609>
- Darwin CR. 1862e.** Letter 3620-Darwin, C. R., to Hooker, J. D., 23 June 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3620>
- Darwin CR. 1862f.** Letter 3628-Darwin, C. R., to Hooker, J. D., 30 [June 1862]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3628>
- Darwin CR. 1862g.** Letter 3662-Darwin, C. R., to Gray, Asa, 23[–4] July 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3662>
- Darwin CR. 1863a.** Letter 4217-Darwin, C. R., to Bentham, George, 19 June 1863. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-4217>
- Darwin CR. 1863b.** Letter 4184-Darwin, C. R., to Crüger, Hermann, 25 May 1863. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-4184>
- Darwin CR. 1863c.** Letter 4047-Darwin, C. R., to Lyell, Charles, 17 March 1863. Downloaded and read in August 2011. Available at: <http://www.darwinproject.ac.uk/entry-4947>
- Darwin CR. 1867a.** Letter 5647-Darwin, C. R., to Samuelson, James, 12 October [1867]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-5647>

- Darwin CR. 1867b.** Letter 5648-Darwin, C. R., to Wallace, A. R., 12–13 October [1867]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-5648>
- Darwin CR. 1904.** *The various contrivances by which orchids are fertilised by insects*. 7th impression of the 2nd edition. London: John Murray. The first printing of the second edition was in 1877.
- Darwin F, ed. 1958.** *The autobiography of Charles Darwin and selected letters*. New York: Dover Publications. With additional editing and restoration by Nora Barlow.
- Denso P. 1943.** Einzeldarstellungen zu madagassischen Schmetterlingen. *Deutsche Entomologische Zeitschrift, Iris* **57**: 102–127.
- du Petit-Thouars LMA-A. 1822.** *Histoire particulière de plantes orchidées recueillies sur les trois îles australes d'Afrique*. Paris: Pépinière du Roi, Faubourg du Roule, no. 20; Arthus Bertrand, Libraires; Treuttel et Wurz, Libraires.
- du Petit-Thouars LMA-A. 1834.** *Notices biographiques sur plusieurs membres de la famille Aubert de Saint Georges Petit Thouars destinées à leurs parents et à leurs amis*. Paris: H. Fournier.
- du Petit-Thouars LMA-A. 1979.** *Histoire particulière de plantes orchidées recueillies sur les trois îles australes d'Afrique*. Facsimile reprint of the 1822 original, New York: Earl M. Coleman.
- Du Puy D, Cribb P, Bosser J, Hermans C. 1999.** *The orchids of Madagascar*. Kew: Royal Botanic Gardens.
- Ellis W. 1858.** *Three visits to Madagascar*. London: John Murray.
- Fay MF, Chase MW. 2009.** Orchid biology: from Linnaeus via Darwin to the 21st century. *Annals of Botany* **104**: 359–364.
- Forbes WA. 1873.** Fertilization of orchids. *Nature* **8**: 121.
- Fowlie JA. 1969.** The curious tryst of the star orchid of Madagascar (*Angraecum sesquipedale*). *Orchid Digest* **33**: 209–210.
- Frownie SA. 2005.** *Fragrant orchids*. Portland: Timber Press.
- Hamilton RE. 1990.** Flowering months of orchids under cultivation. In: Arditti J, ed. *Orchid biology, reviews and perspectives*, vol. V. Portland: Timber Press, 265–405.
- Hillerman FE, Holst AW. 1986.** *An introduction to the cultivated angraecoid orchids of Madagascar*. Portland: Timber Press.
- Hooker JD. 1862a.** Letter 3527-Hooker, J. D. to Darwin, C. R., [17 May 1862]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3527>
- Hooker JD. 1862b.** Letter 3611-Hooker, J. D. to Darwin, C. R., [19 June 1862]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3611>
- Hooker JD. 1862c.** Letter 3624-Hooker, J. D. to Darwin, C. R., 28 June 1862. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-3624>
- Hoot SB. 2009.** Charles Darwin: botanist. *Reports of the National Center for Science Education* **29**: 19–21.
- Jacquet P. 2002.** *Une histoire de l'orchidologie française*. D'Embrun: Société Française d'Orchidophile.
- Jacquet P. 2007.** Orchid discoveries by French botanists around the world. In: Cameron KM, Arditti J, Kull T, eds. *Orchid biology, reviews and perspectives*, vol. IX. *Memoirs of the New York Botanical Garden* **95**: 27–89.
- Jeffrey DC, Arditti J, Koopowitz H. 1970.** Sugar content in floral and extra floral exudates of orchids: pollination, myrmecology and chemotaxonomy implication. *New Phytologist* **69**: 187–195.
- Jermy T. 1999.** Deep flowers for long tongues: a final word. *Trends in Ecology and Evolution* **14**: 34.
- Johnson SD, Edwards TJ. 2000.** The structure and function of orchid pollinia. *Plant Systematics and Evolution* **222**: 243–269.
- Johnson SD, Steiner KE. 1997.** Long tongues fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). *Evolution* **51**: 45–53.
- Kaiser R. 1993.** *The scent of orchids*. Basel: Editiones Roche.
- Kaiser RAJ. 1992.** The scent of orchids. In: Teranishi R, Buttery RG, Sugisawa H, eds. *Bioactive volatile compounds from plants*. Washington, DC: American Chemical Society Symposium Series 525. American Chemical Society, 240–268.
- Kawahara AY, Mignault AA, Regier JC, Kitching IJ, Mitter C. 2009.** Phylogeny and biogeography of hawkmoths (Lepidoptera: Sphingidae): evidence from five nuclear genes. *PLoS ONE* **4**: 1–11.
- Kitching IJ. 2002.** The phylogenetic relationships of Morgan's sphinx, *Xanthopan morgani* (Walker), the tribe Acherontiini, and allied long-tongued hawkmoths (Lepidoptera: Sphingidae, Sphinginae). *Zoological Journal of the Linnean Society* **135**: 471–527.
- Koopowitz H, Marchant TA. 1998.** Postpollination nectar reabsorption in the African epiphyte *Aerangis veridickii* (Orchidaceae). *American Journal of Botany* **85**: 508–512.
- Kritsky G. 2001.** Darwin's Madagascan hawkmoth predication. *American Entomologist* **37**: 206–210.
- Kutschera U, Briggs WR. 2009.** From Charles Darwin's botanical country-house studies to modern plant biology. *Plant Biology* **11**: 785–795.
- Leandri J. 1962.** Henri Perrier de la Bâthie. *Taxon* **11**: 1–3.
- Lecoufle M. 1982.** The *Angraecum sesquipedale* and pollinization. *Orchid Digest* **46**: 99–102.
- Lennox JG. 1993.** Darwin was a teleologist. *Biology and Philosophy* **8**: 409–421.
- Luyt R, Johnson SD. 2001.** Hawkmoth pollination of the African orchid *Mystacidium venosum*, with special reference to flower and pollen longevity. *Plant Systematics and Evolution* **228**: 49–62.
- Luyt R, Johnson SD. 2002.** Postpollination nectar reabsorption and its implication for fruit quality in an epiphytic orchid. *Biotropica* **34**: 442–446.
- Martins DJ, Johnson SD. 2007.** Hawkmoth pollination of aerangecoid orchids in Kenya, with special reference to nectar sugar concentration gradients in the floral spurs. *American Journal of Botany* **94**: 650–659.
- Micheneau C, Fournei J, Gauvin-Bialecki A, Paillet T. 2008.** Auto-pollination in a long-spurred endemic orchid

- (*Jumellea stenophylla*) on Reunion Island (Mascarene Archipelago, Indian Ocean). *Plant Systematics and Evolution* **272**: 11–22.
- Micheneau C, Johnson SD, Fay MF. 2010.** Orchid pollination: from Darwin to the present day. *Botanical Journal of the Linnean Society* **162** (Suppl.): S10–S28.
- Moore D. 1849.** On growing orchids from seeds. *Gardeners' Chronicle* **35**: 549.
- Moore D. 1875.** Design in the structure & fertilisation of plants. In: Johnston WM, ed. *Science and revelation: A series of lectures in reply to the theories of Tyndall, Huxley, Darwin, Spencer, etc.* Belfast: William Mullan, 3–32.
- Moore R. 1957.** *Charles Darwin*. London: Hutchinson & Co.
- Motes M. 2011.** Darwin on orchids. Survival shapes the flower. *Orchids* **80**: 350–355.
- Müller H. 1873.** Probosces capable of sucking the nectar of *Angraecum sesquipedale*. *Nature* **8**: 223.
- Müller H. 1883.** *The fertilisation of flowers*. Translated and edited by D'Arcy W. Thompson with a preface by Charles Darwin. London: MacMillan and Co.
- Nilsson LA. 1988.** The evolution of flowers with deep corolla tubes. *Nature* **334**: 147–149.
- Nilsson LA. 1992.** Orchid pollination biology. *Trends in Ecology and Evolution* **7**: 255–259.
- Nilsson LA. 1998a.** Deep flowers for long tongues. *Trends in Ecology and Evolution* **13**: 259–260.
- Nilsson LA. 1998b.** Deep flowers for long tongues: reply from L. A. Nilsson. *Trends in Ecology and Evolution* **13**: 509.
- Nilsson LA, Jonsson L, Ralison L, Randrianjohany E. 1987.** Angraecoid orchids and hawkmoths in central Madagascar: special pollination systems and generalist foragers. *Biotropica* **19**: 310–318.
- Nilsson LA, Jonsson L, Rason L, Randrianjohany E. 1985.** Monophily and pollination mechanisms in *Angraecum arachnites* Schltr. (Orchidaceae) in a guild of long-tongued hawk-moths (Sphingidae) in Madagascar. *Biological Journal of the Linnean Society* **26**: 1–19.
- Nilsson LA, Rabakonandrianina E. 1988.** Hawk-moth scale analysis and pollination specialization in the epilithic Malagasy endemic *Aerangis ellisii* (Reichenb. fil.) Schltr. (Orchidaceae). *Biological Journal of the Linnean Society* **97**: 49–61.
- Oberthür C. 1920.** *Études de lépidoptérologie comparée*. Fascicule XVII, plate DII. Rennes: Imprimerie Oberthür.
- Oliver D. 1862.** Letter 5647–Oliver, D., to Darwin, C., 14 May 1863. Downloaded and read in April–June 2011. Available at: <http://www.darwinproject.ac.uk/entry-3589>
- Ospina HM. 1969.** Los antipolinizadores. *Orchideologia* (Medellin, Colombia) **4**: 25–27.
- Perrier de la Bâthie H. 1930.** *Catalogue des plantes de Madagascar*. Tananarive: G. Pitot & Co.
- Perrier de la Bâthie H. 1941.** *Flore de Madagascar (Plantes Vasculaires)*, 49^e Famille. *Orchidées (Orchidaceae)*, vol. II. Tananarive: Imprimerie Officielle.
- Perrier de la Bâthie H. 1981.** *Flora of Madagascar*, 49th family–Orchids, vols I and II. English revision and translation by Steven D. Beckman. Lodi: Steven D. Beckman.
- Pinhey E. 1962.** *Hawkmoths of central and south Africa*. London: Longmans.
- Poe y Aloy F. 1832.** *Centurie de Lepidoptere de l'Île de Cuba*. Paris: J. A. Mercklein.
- Richardson EW. 1916.** *A veteran naturalist being the life and work of W. B. Tegetmeier*. London: Witherby & Co.
- Robertson JL, Wyatt R. 1990.** Evidence for pollination ecotypes in the yellow-fringed orchid, *Platanthera ciliaris*. *Evolution* **44**: 121–133.
- Rolfe RA. 1901.** *Angraecum sesquipedale*. *Orchid Review* **9**: 49–50.
- Rothschild LW, Jordan K. 1903.** A revision of the lepidopterous family Sphingidae. *Novitates Zoologicae* **9** (Supplement), cxxxv plus 972 pp. plus 67 plates (*Xanthopan* is on pages 5, 28, 30–33, 817).
- Samuelson J. 1866.** Letter 5049–Samuelson, J., to Darwin, C. R., August 1866. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-5049>
- Samways MJ. 1998.** Letter. *Trends in Ecology and Evolution* **13**: 460.
- Sander F. 1888.** *Reichenbachia*, vol. 1. St. Albans: F. Sander & Co. Facsimile edition, c. 1980 by an unknown publisher.
- Sawyer S. 2011.** Darwin's orchid and Morgan's sphinx moth. *Orchids* **80**: 384.
- Schlechter R. 1925.** *Orchidaceae Perrierianae. Ein Beitrag zur Orchideenkunde der Insel Madagascar*. Repertorium Specierum Novarum Regni Vegetabilis. Beihefte. Vol. 33. Dahlem bei Berlin: Verlag der Repertorios. (Reprint 1980 by Otto Koelz Antiquariat, Hernwaldstr. 6, Koenigstein/Taunus, Germany).
- Schultes RE, Pease AS. 1963.** *Generic names of orchids*. New York: Academic Press.
- Senghas K. 1973.** *Angraecum bosseri*, ein neuer 'Stern von Madagascar'. *Die Orchidee* **24**: 191–193.
- Sprengel CK. 1793.** *Des entdeckte Geheimnis der Natur in Bau und in der Befruchtung des Blumen*. Berlin: Friedrich Vieweg dem Altern (reprint, 1972 by J. Cramer, 3301 Lehre, Germany).
- Stearn WT. 2004.** *Botanical Latin*, 4th edn. Portland: Timber Press.
- Strauss MS. 1976.** The physiology of pollination induced phenomena in the Orchidaceae. PhD Dissertation, University of California, Irvine.
- Strauss MS, Koopowitz H. 1973.** Floral physiology of *Angraecum* I. Inheritance of post-pollination phenomena. *American Orchid Society Bulletin* **42**: 495–502.
- Svensson MGE, Rydell LJ, Töve J. 1998.** Letter. *Trends in Ecology and Evolution* **13**: 460.
- Tegetmeier WB. 1862.** Darwin on orchids. *Wheldon's Register of Facts and Occurrences Relating to Literature, the Sciences, and the Arts* **August 1862**: 38b–39b.
- Van der Niet T, Liltved WR, Johnson SD. 2011.** More than meets the eye: a morphological and phylogenetic comparison of long-spurred, white-flowered *Satyrium* species (Orchidaceae) in South Africa. *Botanical Journal of the Linnean Society* **166**: 417–430.
- Van der Pijl L, Dodson CH. 1966.** *Orchid flowers, their*

- pollination and evolution*. Coral Gables, FL: University of Miami Press.
- Veitch J, and Sons. 1887–1894.** *A manual of orchidaceous plants, vol II Vandae-Cypripedieae*. Chelsea: James Veitch & Sons, Royal Exotic Nursery (reprint 1963 by A. Asher & Co., Amsterdam).
- Walker F. 1856.** *List of the specimens of lepidopterous insects in the collection of the British Museum*. Part VIII.—Sphingidae. London: The Trustees of the British Museum.
- Wallace AR. 1867a.** Creation by law. *The Quarterly Journal of Science* **4**: 471–488.
- Wallace AR. 1867b.** Letter 5637-Wallace, A. R. to Darwin, C. R. 1 October [1867]. Downloaded and read in April–May 2011. Available at: <http://www.darwinproject.ac.uk/entry-5637>
- Wallace AR. 1870.** *Contributions to the theory of natural selection*. London: Macmillan & Co.
- Wasserthal LT. 1993.** Swing-hovering combined with long tongue in hawkmoths, an antipredator adaptation during flower visits. In: Barthlott W, Naumann CM, Schnidt-Loske K, Schuchmann KL, eds. *Animal–plant interaction in tropical environments*. Annual Meeting of the German Society for Tropical Ecology. Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig, 77–87.
- Wasserthal LT. 1996.** Of hawkmoth species with long ‘tongues.’ Tropical biocenoses. *Reports of the German Research Foundation [Deutsche Forschungsgemeinschaft (DFG)]* **1**: 22–25.
- Wasserthal LT. 1997.** The pollinators of the Malagasy star orchids *Angraecum sesquipedale*, *A. sororium*, and *A. compactum* and the evolution of extremely long spurs by pollinator shift. *Botanica Acta* **110**: 343–359.
- Wasserthal LT. 1998.** Deep flowers for long tongues. *Trends in Ecology and Evolution* **13**: 459–460.
- Wasserthal LT. 2009.** Bungee jumping spiders challenge Darwin’s hypothesis of a coevolutionary race between long spurred orchids and long tongued moths. *Annual Meeting of Deutsche Zoologische Gesellschaft*, Regensburg. P.67.
- Whittall JB, Hodges SA. 2007.** Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* **447**: 706–709.
- Yam TW, Arditti J, Cameron KM. 2009.** ‘The orchids have been a splendid sport’—an alternative look at Charles Darwin’s contribution to orchid biology. *American Journal of Botany* **96**: 2128–2154.