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Tansley Review No. 110

Numerical and physical properties of orchid seeds and their biological implications

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SUMMARY

Orchid seeds are very small, extremely light and produced in great numbers. Most range in length from *c.* 0.05 to 6.0 mm, with the difference between the longest and shortest known seeds in the family being 120-fold. The 'widest' seed at 0.9 mm is 90-fold wider than the 'thinnest' one, which measures 0.01 mm (because orchid seeds are tubular or balloon-like, 'wide' and 'thin' actually refer to diameter). Known seed weights extend from 0.31 µg to 24 µg (a 78-fold difference). Recorded numbers of seeds per fruit are as high as 4 000 000 and as low as 20–50 (80 000–2 000 000-fold difference). Testae are usually transparent, with outer cell walls that may be smooth or reticulated. Ultrasonic treatments enhance germination, which suggests that the testae can be restrictive. Embryos are even smaller: their volume is substantially smaller than that of the testa. As a result, orchid seeds have large internal air spaces that render them balloon-like. They can float in the air for long periods, a property that facilitates long-distance dispersal. The difficult-to-wet outer surfaces of the testa and large internal air spaces enable the seeds to float on water for prolonged periods. This facilitates distribution through tree effluates and/or small run-off rivulets that may follow rains. Due to their size and characteristics, orchid seeds may also be transported in and on land animals and birds (in fur, feathers or hair, mud on feet, and perhaps also following ingestion).

Key words: orchids, orchid seeds, orchid dispersal, dust seeds, seed floatation, seed production, seed size, seed numbers.

I. INTRODUCTION

Orchids seeds are unique. They differ from those of most angiosperms and resemble the so-called 'dust

seeds' of other plants (Fleischer, 1929, 1930; Ziegenspeck, 1936; Hoene, 1945; Rauh *et al.*, 1975; Rasmussen, 1995). This term probably has its origins as a direct or literal, but not a contextual, translation of the German 'staubförmiger Samen' or 'Staub-Samen'. 'Dust seeds' as a term sounds odd in English and may not be completely descriptive, but it is generally accepted, defined to some extent, and in

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common use – it simply means that the seeds are small. For a more extensive discussion of terminology see Rauh *et al.* (1975) and Barthlott (1976). The seeds were first drawn by the Swiss naturalist Conrad Gesner sometime between 1540 and his death in 1565 (Jacquet, 1994). Since that time, descriptive studies of the seeds form a colourful history (Box 1). Developmental, structural, anatomical, morphological, physiological, ecological, symbiotic and horticultural aspects are discussed elsewhere (Mutsuura *et al.*, 1962; Vij *et al.*, 1981; Weatherhead *et al.*, 1986; Arditti, 1992). The present review will deal only with the purely numerical and physical characteristics of orchid seeds and their biological implications (Figs 1–9; Tables 1–6).

II. NUMBER

Among the best known and most frequently mentioned characteristics of orchids are their small (Figs 1–4; Table 1) and very light (Tables 1–3) seeds, which are usually produced in large numbers (Table 2; Darwin, 1904; Burgeff, 1936; Arditti, 1967, 1979, 1992; Arditti & Ernst, 1984; Rasmussen, 1995). To this day one of the most interesting and perceptive discussions of orchid seed number is by Charles Darwin (Box 2). It is important here as a classic backdrop for modern considerations.

Calculations like Darwin's can result in astronomical numbers (Box 2). Production of large numbers of seeds has been described as a common characteristic in plants that have very specific germination requirements, such as mycotrophy (Rauh *et al.*, 1975; Rasmussen, 1995). These numbers ensure that at least a few seeds will germinate and perpetuate the species – even if Darwin took a dim view of the 'contrivance'. Both the large number and the physical characteristics of orchids facilitate extensive coverage of areas around the seed parent and wider dispersion further away. A consequence of such dispersal is colonization of new and existing favourable sites (Nakamura & Hamada, 1978; Rasmussen, 1995; Murren & Ellison, 1996, 1998; Tremblay, 1997; Carey, 1998; Kull, 1998, Light & MacConaill, 1998; Neiland & Wilcock, 1998; for reviews of evolutionary implications of the nature of orchid seeds see Benzing, 1981, 1987).

It is possible to argue that the production of so many seeds is wasteful of resources and risky, because evolution is unforgiving of waste. Such arguments must be posited against the fact that the orchids are evolutionarily very successful. This success indicates that the survival benefits of begetting many small seeds outweigh the cost of producing them. According to one estimate, the fruit-set in *Cypripedium calceolus* (Figs 3, 7, 8; Tables 1, 2) on the clone level is essentially cost free because ramets that bear fruits 'stay in leaf longer

[and this brings about] compensation on the annual ramet level [because of] its extended growing period' (Kull, 1998). Altogether it seems that regardless of the input by individual plants, the resources devoted to the production of many small seeds by orchid species are a good investment. Moreover, orchid embryos are small (Table 1), some consisting of only a few cells; most have no endosperm (Weiss, 1916; Burgeff, 1936; Arditti & Ernst, 1984; Arditti, 1967, 1979, 1992). Their food reserves consist of cellular inclusions like oil droplets and starch grains at levels that are not high in absolute terms. This means that the resources invested by orchids in the production of numerous seeds may not be as large and wasteful as they seem. Even if not cost-free as in *Cypripedium calceolus* (Fig. 3; Tables 1, 2) the resources expended by orchids may be the same or perhaps even smaller than those invested by other plants in fewer but larger seeds with more reserves.

A comparison between orchid seeds and coconuts (i.e. the seeds of coconut trees) may be instructive. Coconuts are an excellent contrast for orchids because the trees produce relatively few large seeds, which also have lipid reserves. A comparison with medium-sized lipid-containing seeds produced in larger numbers than coconuts (sunflowers or peanuts, for example) would provide less of a contrast. Also, the lipid content of orchids and coconuts is similar. As far as we can determine, comparisons of this type for orchids have not been reported previously. Such comparisons would gain much if data on resources committed to seed production could be related to annual productivity, the locales of seed germination and the likelihood of biophagy. Unfortunately there are not enough published data for more advanced comparisons.

Capsules of *Cycnoches ventricosum* var. *chlorochilon* contain 4000000 seeds (Tables 2, 3) each weighing 3.6 µg. The total weight is 14.4 g seeds fruit⁻¹. Assuming that these seeds contain as much lipid energy as fresh coconut solid endosperm (1470 kJoules 100 g⁻¹) the total is still a minuscule 212 kJoules 14.4 g⁻¹ or 0.000419618 kJoules seed⁻¹. This assumption is justified by findings that show that orchid seeds are fatty in nature (as are coconuts) and may contain as much as 32% lipids (Knudson, 1929; Arditti, 1967, 1979, 1992; Harrison, 1977; Harrison & Arditti, 1978; Arditti & Ernst, 1984).

Fresh solid coconut endosperm ('meat') contains 34% fat and 212 kJoules 14.4 g⁻¹ (Diem, 1962). A nut purchased at random in a food store had 380 g 'meat' (5586 kJoules; 26 times as many as a *Cycnoches* seed). It also contained 120 g of liquid endosperm ('coconut water'). Coconuts fresh off a tree contain more 'water.' This liquid is also energy rich and contains a variety of substances such as vitamins, hormones, amino acids and lipids. Thus the total energy content of a coconut, excluding the shell and outer husk, may be as high as 6000 kJoules,

Box 1. *A historical perspective*

After first being drawn by Gesner (also referred to as Gessner, Gesnerus and Gesneri, 1516–1565; for a likeness see Jaquet, 1994) in the middle of the 16th century, there have been many descriptive studies of orchids undertaken. These first illustrations were intended to be part of *Historia Plantarum*, a book that Gesner planned as a companion for his remarkable *Historia Animalum*. Gesner's early death from the plague prevented completion and publication of *Historia Plantarum*. It also started some of the plates and the manuscript on a two centuries-long odyssey that ended with publication between 1751 and 1759. The tribulations of another set of plates were even longer. They were lost, found in the library of the University of Erlangen (Germany) only after World War II and published between 1972 and 1980 (i.e. about 450 years after they were painted).

Until very recently the existence of drawings of orchid flowers, fruits and seeds (some of them magnified) in Gesner's *Historia Plantarum* was not widely known. Awareness of the seed drawings in the University of Erlangen lost plates was more limited even after they were published. A recent survey (J. Arditti, unpublished) found several plates that contain paintings of seeds.

Georgius Everhardus Rumphius (c. 1627–1702, for a portrait see Arditti, 1984), the so-called Blind Seer of Ambon (an island in the Maluku, formerly Moluccas, Archipelago or Spice Islands, Indonesia), described orchid seeds in his *Herbarium Amboinense* as a 'yellow flour... largely shed and blown away on the wind' (de Wit, 1977). *Herbarium Amboinense* also had a long odyssey (de Wit, 1977). The original was lost in a fire that nearly destroyed the entire city of Ambon. It was reconstituted by assistants because by then Rumphius was blind. The new set was sent to Batavia (now Jakarta) in 1690, copied there for the personal use of the Dutch Governor General and shipped to Holland in 1692. It was lost at sea when the ship that carried it, the *Waterland*, was sunk by the French. Another copy was made from the one owned by the Governor General. It was shipped to Holland in parts. The complete manuscript reached Amsterdam in 1696–1697. Permission to publish was granted c. 1736 to Johannes Burman (1706–1779), Professor of Botany at the University of Amsterdam for 51 years starting in 1728 (his son Nikolaus Laurens Burman, 1734–1793, was also a professor in the same university from 1769 until his death). Burman published six volumes between 1741 and 1750. A companion volume, the *Actuarium*, was published in 1755. Thus, the first description of orchid seeds by Gesner was published 20 years after the second one by Rumphius. However, Gesner's drawings remain the first illustrations of orchid seeds that are known to have been published. Rumphius drew orchid fruits, but never very small flowers and seeds. One reason for this may have been his failing eyesight.

A third set of orchid paintings that includes seeds was also published after a long delay (150 years) in a limited edition of very large and heavy books which are not easily accessible. These books report some of the findings of a Spanish scientific expedition to New Grenada led by José Celestino Bruno Mutis y Bogio (1732–1808). The expedition surveyed the flora of what is now Colombia. Its artists produced more than 200 plates of orchids between 1783 and 1816. The plates languished until the first (introductory) volume in a projected multi-volume series dealing with the Mutis expedition was published (Perez-Arbelaez *et al.*, 1954). Three volumes containing orchid plates were published after that (Schweinfurth *et al.*, 1963; Schweinfurth *et al.*, 1969; Fernandez Perez, 1985). More are to be published. Some of the plates contain excellent paintings of different stages of fruit development, maturation and dehiscence. There are also cross- and longitudinal-sections of fruits that show seeds as white fluffy masses, brown lines and/or dark dots. A number of plates contain drawings of seeds, some small and described as being natural size, others are magnified. Several of the 'natural size' line drawings of fusiform seeds have dots in their middle (and widest) part, which obviously represent embryos. A number of the greatly magnified illustrations of seeds are inaccurate because they look like woolly or fluffy, narrow and pointed ellipses. Small line drawings which show seeds that look like drops or apostrophes also seem unrealistic.

All illustrations in the *Flora de la Real expedicion Botanica del Nuevo Reino de Granada* were made after the publication of *Herbarium Amboinense* and *Historia plantarum*, but they are still among the earliest representations of orchid seeds (second drawings after Gesner's and third descriptions following *Herbarium Amboinense* and *Historia Plantarum*). They are probably the first clearly to indicate size. The third, as well as most accurate in terms of size and appearance are attractive colour paintings of orchid seeds (Fig. 1a–c), made and published in Austria (Beer, 1863). Strangely, relatively few colour paintings of orchids were published during the last century, but there is an abundance of line drawings with proper size indications (Bernard 1909; Burgeff, 1936; Arditti, 1992; Rasmussen, 1995). Hans Burgeff (1883–1976) was the first to provide weights determined with relatively modern equipment and to measure floatation times (Burgeff, 1936). His measurements were extended through determination of seed volume and air space (Arditti *et al.*, 1979, 1980; Healey *et al.*, 1980).

Photographs (standard, macro and micro) started to appear in the literature as appropriate photographic equipment became available. Due to their dimensions and shape, orchid seeds are difficult to photograph because of greatly reduced depth of field at appropriate magnifications. The first SEM photographs were published in the mid-1970s by W. Barthlott and his associates in Germany. Other SEM studies, structural, morphometric and taxonomic, followed (e.g. Arditti *et al.*, 1979, 1980; Healey *et al.*, 1980; Chase & Pippen, 1988, 1990). The first descriptions and drawings of orchid seedlings were published in 1804 by the British botanist R. A. Salisbury (for a photograph see Arditti, 1984).

Horticultural attempts to germinate orchid seeds date back to the mid-1800s. The first success was reported in 1849 by David Moore (1807–1879, for a portrait see Arditti, 1984), Director of the Glasnevin Botanic Gardens in Ireland (he wrote religion-based anti-Darwin tracts during his later years) and by two British gardeners, J. Cole and R. Gallier, later in the same year. In 1899 Noël Bernard (1874–1911, for photographs and a short biography see Arditti, 1984, 1990), Professor of Botany at the University of Caen, France became the first to describe the role of mycorrhiza in orchid seed germination. Lewis Knudson (1884–1958, for photographs and a biography see Arditti, 1984, 1990), Professor of Botany at Cornell University, formulated methods for asymbiotic germination. He first published his method in 1921 in Spain, in the Spanish language in an (at least presently) obscure journal (Arditti, 1984, 1990, 1992; Jaquet, 1994).

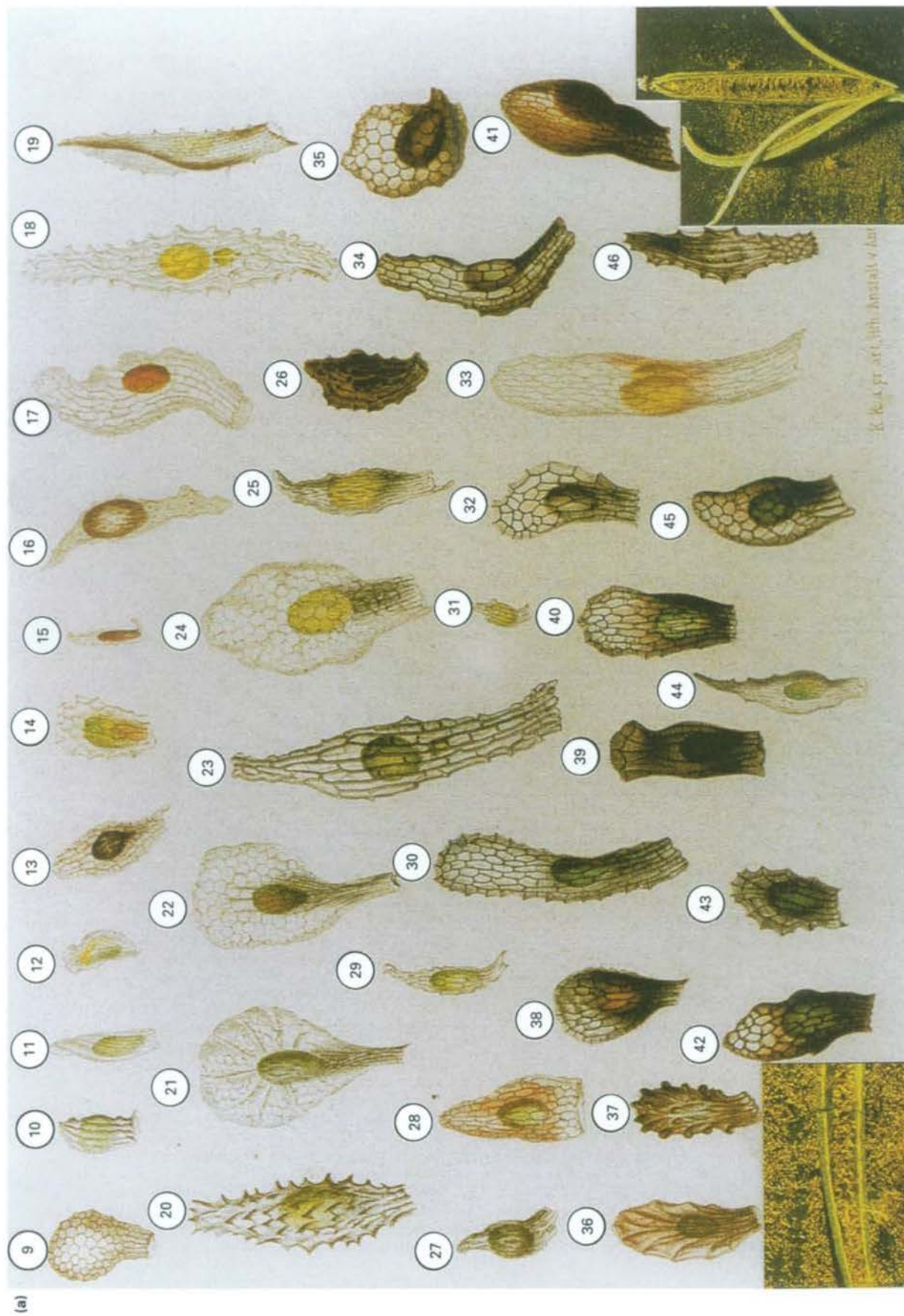


Fig. 1a. For legend see page 372.

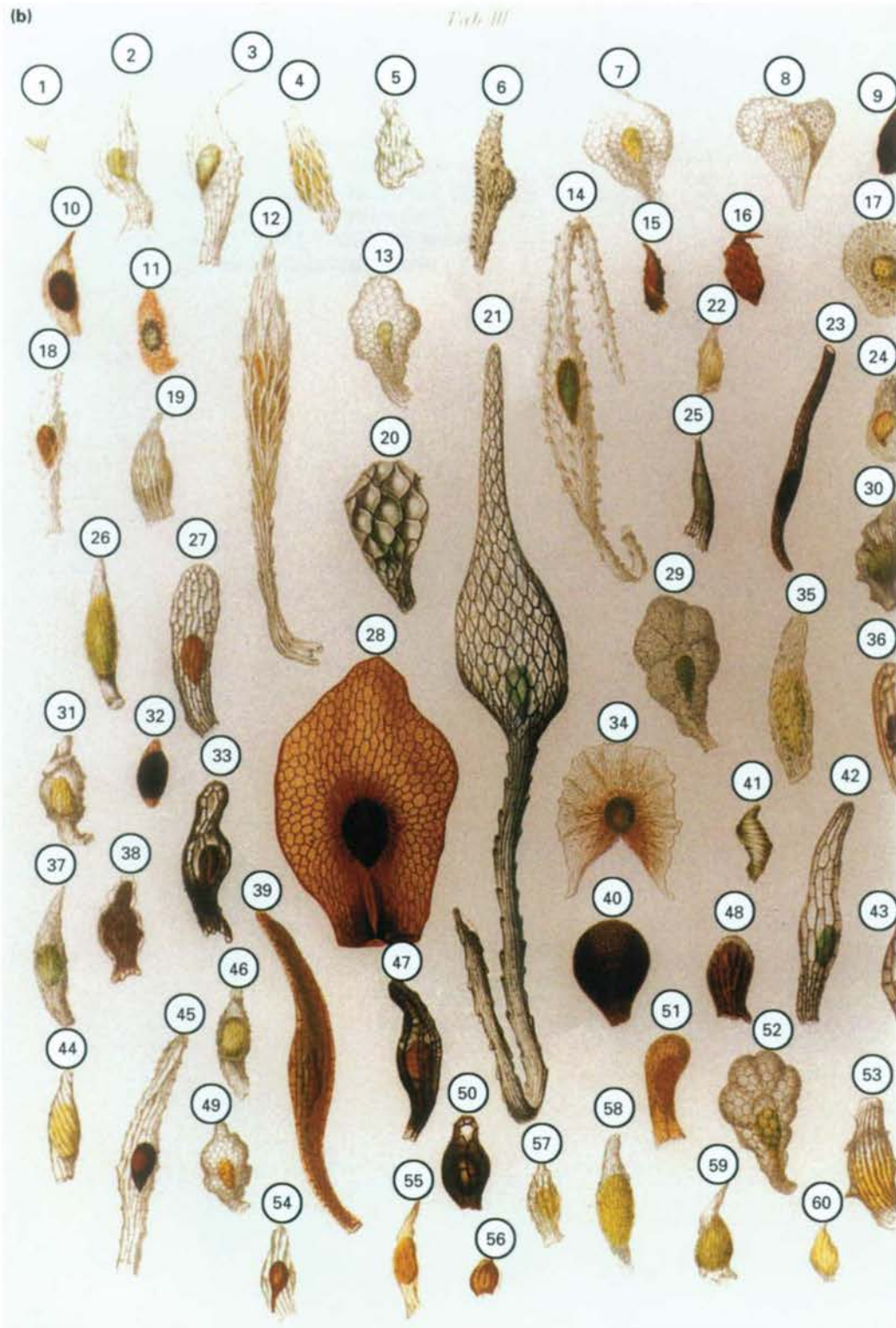


Fig. 1b. For legend see page 372.

which would be the content of 113 207 547 *Cynoches* seeds (or 2.83 times the number of seeds found in a single capsule; this orchid probably produces more than one capsule per plant only rarely, if at all). Coconut trees may produce up to 75 fruits per plant,

but a reasonable average is 25. If so, 160 000 trees would be needed to produce 4 000 000 seeds, which will contain 24 000 000 000 kjoules in the 'water' and 'meat' alone. Not all orchid seeds produce mature plants, but the same is true for coconuts. Therefore



Fig. 1c.

Fig. 1. (Legends for (a-c)). Paintings and photographs of orchid seeds. Note that the first name used in each case is the name in the original source; some current names are also given to ensure accuracy (it is not uncommon to have several taxa lumped into a single concept or one species split into more than one taxon), facilitate identifications and make possible correlations between seed characteristics and different classification approaches. (a) Circled nos. 1-38: 1, *Sturmia loesseli* (now *Liparis loesseli*); 3, *Octomeria lancifolia*; 4, *Maxillaria crocea*; 5, variety of *Dactylorhiza* (*Orchis*) *maculata*; 6, *Gymnadenia conopsea*; 7, *Angraecum bilobum* (now *Aerangis biloba*, or *Aerangis kirkii*); 8, *Phajus albus* (now known as *Thunia alba*); 9, *Stanhopea tigrina* var. *superba*; 9, *Listera ovata*; 10, *Mormodes buccinator*; 11, *Barkeria melanocaulon*; 12, *Mormodes viridiflora*; 13,

the energy cost per mature offspring is much lower for the orchid. Clearly energy investment in the future of the species by *C. ventricosum* var. *chlorochilon* is more efficient than that of coconuts. Similar

comparisons with other fatty seeds should prove interesting.

Another benefit of the relatively small energy investment in numerous seeds by the orchid is the

Stanhopea warczewitzii; 14, *Stanhopea tigrina*; 15, *Mormodes pardina* var. *unicolor* (now *Mormodes maculatum*); 16, *Stanhopea aurea* (now *Stanhopea wardii*); 17, *Listera ovata*; 18, *Himantoglossum hircinum*; 19, *Tetragamestus modestus* (genus now known as *Scaphyglottis*). 20, *Orchis longicornu*; 21, *Ornithocephalus*; 22, *Corallorhiza innata*; 23, *Scaphyglottis vestita*; 24, *Orchis maculata* (*Dactylorhiza maculata*); 25, *Epipactis latifolia*; 26, *Pyrola rotundifolia* (this is not an orchid – it belongs to the Pyrolaceae); 27, *Orchis coriophora*; 28, *Orchis secundiflora*; 29, *Odontoglossum sphacelatum* (now *Oncidium sphacelatum*); 30, *Orchis fragrans*; 31, *Orchis brevicornu* (correct specific epithet is *brevicornis*; species now known as *Orchis patens*); 32, *Orchis latifolia* (now *Dactylorhiza majalis*); 33, *Neottia nidus-avis*; 34, *Nigritella angustifolia* (now *Nigritella nigra*); 35, *Orchis intacta* (now *Neotinea*); 36, *Epidendrum stamfordianum*; 37, *Gymnadenia longifolia*; 38, *Cypripedium barbatum* (now *Paphiopedilum barbatum*). The insert at bottom left shows magnified seeds inside an opened *Sarcochilus* capsule; the insert at bottom right shows a dehiscent fruit of *Sarcochilus* at about natural size. (b) Circled nos. 1–60: 2, *Calanthe veratrifolia*; 3, *Phajus grandifolius* (now *Phaius tankervilleae*); 4, *Zygopetalum mackayi*; 5, *Zygopetalum intermedium*; 6, *Bletia sheperdii* (now *Bletia verecunda*); 7, *Stanhopea insignis*; 8, *Stanhopea oculata*; 9, *Thelymitra ixioides*; 10, *Leptotes bicolor*; 11, *Promenaea stapelioides*; 12, *Govenia lilacina* (correct name is *Govenia liliacea*); 13, *Gongora maculata* var. *pallida*; 14, *Sobralia liliastrum*; 15, *Aerides odoratum*; 18, *Cattleya amethystina* (now *Cattleya intermedia*); 19, *Dicrypta glaucescens* var. Hort. (genus now known as *Maxillaria*); 20, *Eulophia streptopetala*; 21, *Epidendrum cinnabarinum*; 22, *Miltonia morelliana* (now *Miltonia spectabilis* var. *morelliana*); 23, *Goodyera procera*; 24, *Acropera loddigesii* (now *Galeola galeata*); 25, *Brassia cowanii* (now *Brassia verrucosa*); 26, *Cattleya bicolor*; 27, *Cymbidium odontorhizon* (several reference works do not list such an orchid); 28, *Epistephium parviflorum*; 29, *Gongora bufonia*; 30, *Acropera* (*Gongora*) *luteola*; 31, *Acropera maculata* (now *Gongora quinquenervis*); 32, *Luisia teretifolia*; 33, *Orchis acuminata* (at one time this orchid was classified as *Orchis tridentata* var. *lactea*; more recently it was listed as *Orchis lactea*); 34, *Haematorchis altissima* (at one time *Galeola altissima* and now *Erythorchis altissima*); 35, *Odontoglossum bictoniense*; 36, *Habenaria tridentata*; 37, *Epidendrum cochleatum*; 38, *Coricium crispum* (genus has been/is also known as *Pterygodium*, *Ommatodium* and *Anochilus*); 38, *Orobanche*, *Orobanchaceae* (broomrape, a non-orchidaceous plant); 39, *Goodyera discolor* (now *Ludisia discolor*); 40, *Vanilla planifolia*; 41, *Odontoglossum pulvinatum* (actually *Oncidium pulvinatum*); 42, *Phajus maculatus* (now *Phaius flavus*); 43, *Phajus bicolor* (now *Phaius tankervilleae*); 44, *Trichopilia albida* (now known as *Trichopilia fragrans*); 45, *Neottia speciosa* (now *Stenorhynchus speciosa*); 46, *Epidendrum lancifolium* (now *Epidendrum cochleatum*); 47, no caption in original; 48, *Habenaria hispidula*; 49, *Triphora pendula* (several sources treat *Triphora* as a synonym of *Pogonia*); 50, *Corycium orobanchoides* (also known as *Pterygodium orobanchoides*); 51, *Neottia aestivalis* (now *Spiranthes aestivalis*); 52, *Cirrhaea viridi purpurea* (may well be a hybrid between *Cirrhaea viridifusca* and *Cirrhaea purpurascens*; the other names for this genus, *Scleropteris* and *Sarcoglossum*, go in and out of fashion); 53, *Acropera citrina* (now *Gongora galeata*); 54, *Disperis villosa*; 55, *Sarcanthus rostratus* (genus now part of *Cleisostoma*, the species was also known as *Vanda recurva* and *Vanda rostrata*); 56, *Dicrypta tenella* (genus now known as *Maxillaria*); 57, *Promenaea rollinsonii*; 58, *Cattleya tigrina* (now *Cattleya guttata*); 59, *Dicrypta glaucescens* (genus now known as *Maxillaria*); 60, *Sarcanthus violacea* (one possibility is that this is now *Rhyncostylis violacea*, which was variously known as *Anota violacea*, *Saccolabium violaceum* and *Vanda violacea* – there is a very large number of transfers between these genera). (c) Circled nos. 1–60: 1, *Pholidota rubra* (current name unknown); 2, *Epidendrum ramosum*; 3, *Goodyera repens*; 4, *Goodyera semipelucida*; 5, *Neottia pubescens* (now a synonym of *Goodyera pubescens*); 6, *Laelia galeottiana* (current name unknown); 7, *Gamoplexis orobanchoides* (*Gamoplexis* is a synonym of *Gastrodia*); 8, *Epidendrum crassifolium* (but also *Epidendrum crassifolium* and *Epidendrum ellipticum*); 9, *Sobralia decora*; 10, *Habenaria dilatata* (now *Platanthera dilatata*); 11, *Otochilus fusca*; 12, *Dendrobium plicatile* (now *Flickingeria fimbriata*); 13, *Cerathandra chloroleuca* (genus name is spelled *Ceratandra*; present name *Ceratandra atrata*); 14, *Disa cernua*; 16, *Cyrtosia lindleyana* (current genus name unknown); 17, *Cattleya crispa* (now *Laelia crispa*); 19, *Xylobium squalens*; 20, *Laelia anceps*; 21, *Epidendrum ciliare*; 22, *Satyrium nepalense*; 23, *Disa cornuta*; 24, *Sobralia macrantha*; 25, *Huntleya violacea* (also known as *Bollea violacea*); 26, *Ophrys funerea* (a synonym of *Ophrys fusca*); 27, *Pleurothallis sessiliflorum* (current name unknown); 28, *Satyrium carneum*; 29, *Acanthophippium bicolor*; 30, *Cymbidium sinense*; 31, *Cattleya harrisonii* (now *Cattleya harrisoniana*); 32, *Agraphyllum* sp.; 33, *Stanhopea violacea*; 34, *Phajus wallichii* (synonym of *Phaius tankervilleae*); 35, *Selenipedium schlimii* (now a synonym of *Phragmipedium schlimii*); 36, *Laelia perinmii*; 37, *Epidendrum papillosum* (or *Encyclia alata*); 38, *Isochilus lineraris*; 39, *Cattleya loddigesii*; 40, *Cattleya forbesii*; 41, *Malaxis liliifolia* (now a synonym of *Liparis liliifolia*); 42, *Disa pulchella*; 43, *Neottia vitalis* (current name unknown); 44, *Trichocentrum fuscum*; 45, *Epidendrum stamfordianum* var. *carnea*; 46, *Dendrobium cretaceum*; 47, no caption in original; 48, *Pterygodium inversum*; 49, *Pelexia adnata* (current name unknown); 50, *Pterygodium volucre* (correct name *Pterygodium volucris*); 51, *Pterygodium catholicum*; 52, *Acroclaene punctata*; 53, *Vanda coerulea*; 54, *Brassavola cordata*; 55, *Apaturia senilis* (correct spelling *Apatura*; since at present this genus is considered to be a synonym of *Pachystoma*, the species name becomes *Pachystoma senile*, which in turn is reduced to synonymy under *Pachystoma pubescens*); 56, *Dicrypta bauerii* (now *Maxillaria crassifolia*); 57, *Satyrium bicallosum* (current name unknown); 58, *Lycaste harrisonii* (correct name *Lycaste harrisoniae*; now *Bifrenaria harrisoniae*); 59, *Otochilus porrecta*; 60, *Aerides* sp. Seed paintings ($\times 100$ in the original) are from Beer, 1863. Magnifications here are: (a) $\times 109$; 1(b) $\times 84$; 1(c) $\times 81$. Original colour prints, reprinted, with permission, from Arditti (1993). Photographic inserts in (a) are from Upton (1992), which does not provide a magnification factor.

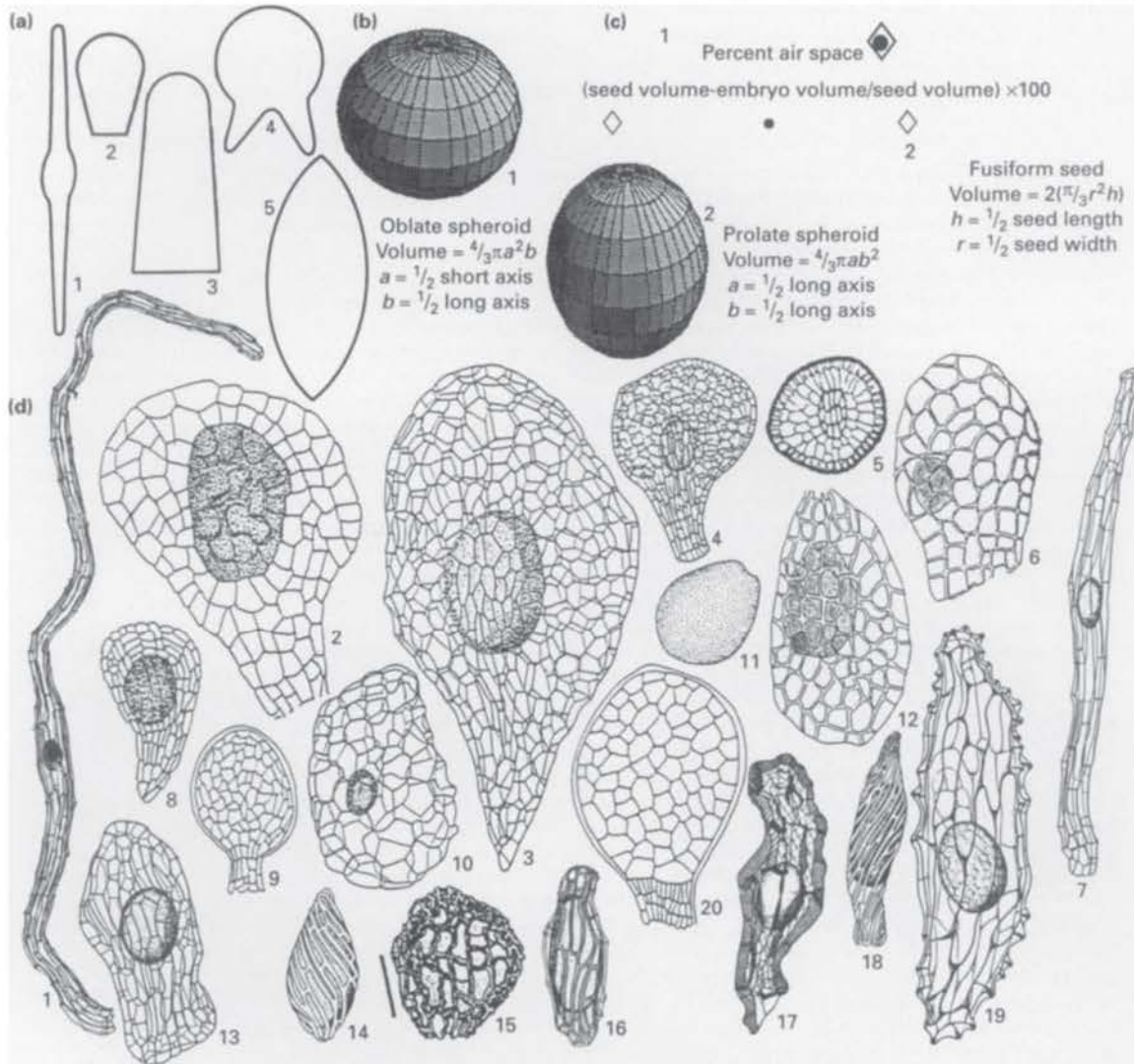


Fig. 2. Orchid seeds and embryos: general shapes, geometry and line drawings. (a) Five general shapes into which orchid seeds have been classified (Clifford & Smith, 1969). The most common are shapes 1 and 5. They are followed by forms 2 and 3. Form 4 is relatively rare. Form 5, unidentified. (b) Orchid embryos are prolate (1) not oblate (2) spheroids. (c) Fusiform orchid seeds: formula and diagram of percent free air space (1), together with formula used to calculate the volume of this form (2). (d) Line drawings of orchid seeds: 1, *Acanthephippium sylhetense*, $\times 75$; 2, *Stanhopea tigrina*, magnification unknown; 3, *Stanhopea oculata*, $\times 150$; 4, *Stanhopea oculata*, magnification unknown (two drawings from different sources are presented here to show that there is variability in seed form and size); 5, *Vanilla planifolia*, cross section diameter 0.367 mm; 6, *Listera australis*, $\times 97$; 7, *Haemaria discolor* (now *Ludisia discolor*), $\times 89$; 8, *Pleione formosana* (now *Pleione bulbocodioides*), magnification unknown; 9, *Zygopetalum intermedium*, magnification unknown; 10, *Epipogium nutans* (now *Epipogium roseum*), $\times 166$; 11, *Vanilla planifolia*, magnification unknown; 12, *Listera convallarioides*, $\times 97$; 13, *Liparis loeselii*, $\times 113$; 14, *Vanda*, $\times 80$; 15, *Schizochilus zeyheri*, bar, 0.1 mm; 16, *Lycaste skinneri*, $\times 111.5$; 17, *Serapias cordigera*, $\times 83$; 18, *Dendrobium*, $\times 108$; 19, *Catasetum macrocarpum*, $\times 128$; 20, *Stanhopea saccata*, magnification unknown. Sources: 1, 3, 5, 7, 10, 12, 13, 14, 17, 16, 18, 19 – Burgeff, 1936; 4, 11 – Poudubnaya-Arnoldi & Selezneva, 1957b; 2, 8, 9, 20 – Cherevchenko & Kushnir, 1986; 6, 11 – Curtiss, 1893; 15 – Kurzweil, 1993.

minute size and unique structure of these seeds. Coconuts, being large, heavy, with a hard shell and spongy husk, can only be dispersed through transport on land (which is not always easy for a fruit of this nature) or floatation (sometimes for prolonged periods in oceans with no certainty of reaching suitable land). However, orchid seeds can be transported on, and perhaps in, the bodies of land animals

(fur, hair, mud on parts of the body) and birds (feathers or mud on their feet) as well as by floatation in water or air (Went, 1957; Gandawijaja & Arditto, 1983; Arditto, 1992).

Altogether, orchids derive important survival benefits from a penurious approach to seed production. Individual capsules may contain many seeds (Table 2), but some species and populations set fruit

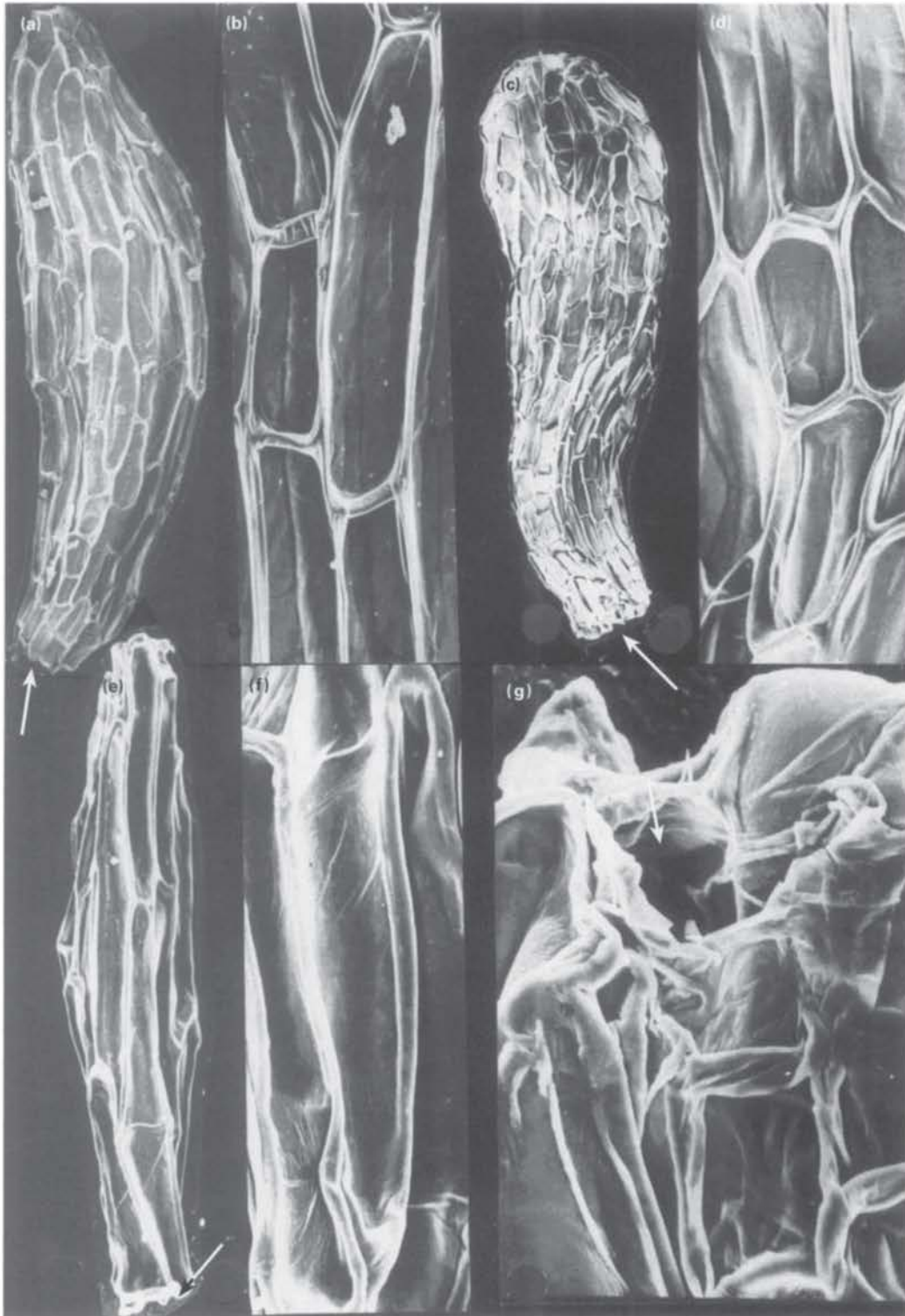


Fig. 3. SEMs of mature seeds (a,c,e), testa cell walls (b,d,f,g) and suspensor end openings (arrows in a,c, e and g) of *Cypripedium calceolus* var. *parviflorum* (a, $\times 110$; b, $\times 465$), *Cypripedium reginae* (c, $\times 55$; d, $\times 4600$) and *Paphiopedilum* cv. Susan Tucker \times *Paphiopedilum parishii* (e, $\times 327$; f, $\times 780$; g, $\times 1200$). Testa cell walls are smooth or nearly so. In (g), the opening in the suspensor end of the seed that is shown is wide enough to allow entry of water and fungal hyphae. *Reproduced, with permission, from Arditti et al. (1979).*

sparingly, one example being *Lepanthes caritensis* (Tremblay, 1997). Recent studies have shown that there are several factors that limit fruit set and seed

production in orchids (Willems, 1992). Pollinator availability is one such factor in the following: *Aspasia principissa* (Zimmerman & Aide, 1989);

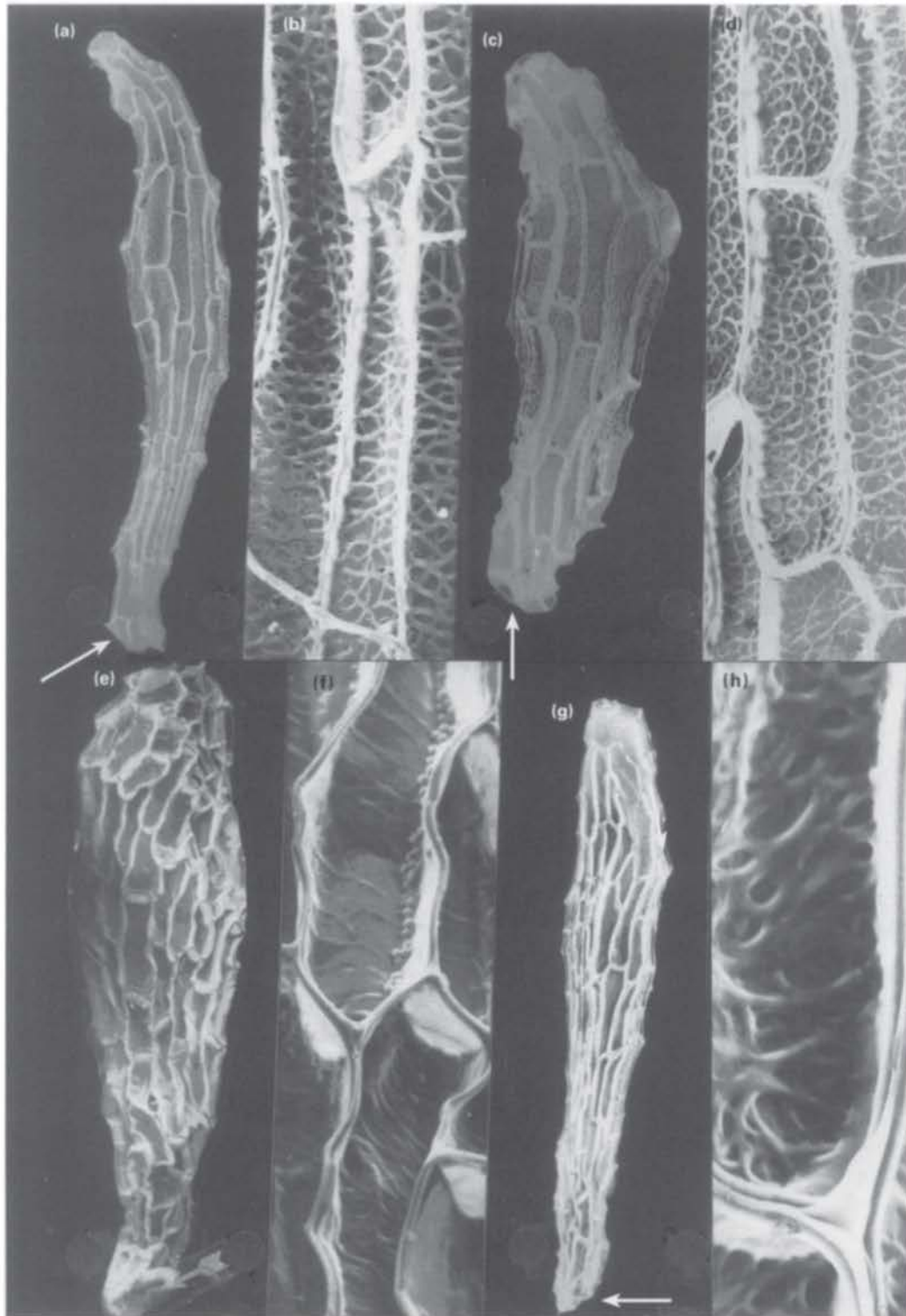


Fig. 4. SEMs of intact seeds (a,c,e,g), testa cell walls (b,d,f,h) and suspensor end openings (arrows in a,c,e,g) of California (a, $\times 135$; b, $\times 862$) and Colorado (c, $\times 260$; d, $\times 673$) plants of *Calypso bulbosa*. Testa cell walls (b,c) are reticulated, but reticulations as well as seed shape and size from the two populations are different. The California seeds are mature, those from Colorado are not. Seeds of *Corallorhiza maculata* (e-h: e, $\times 100$; f, $\times 47$; g, $\times 90$; h, $\times 1200$) differ in shape and reticulations. *Reproduced, with permission, from Arditti et al. (1980).*

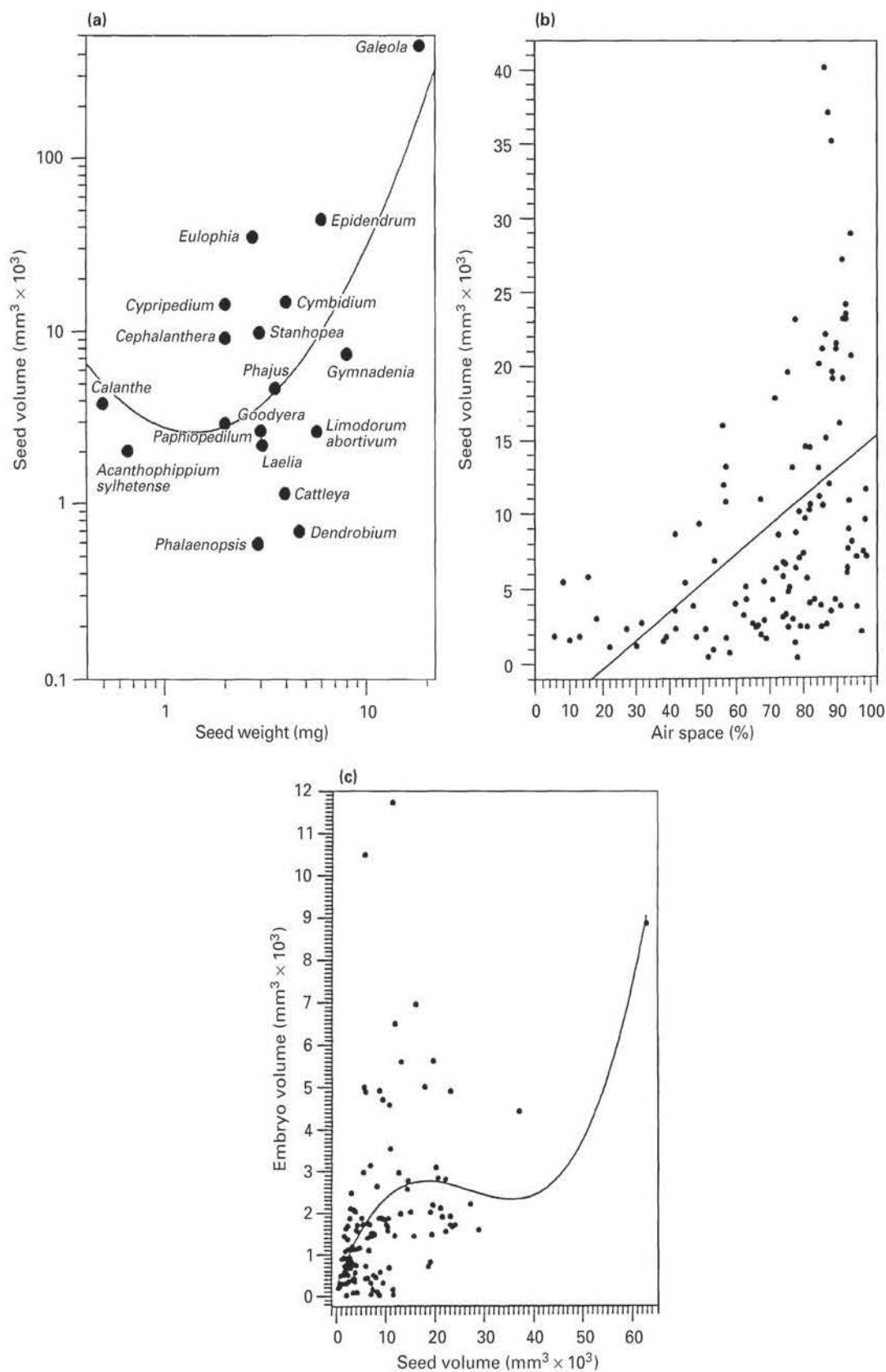


Fig. 5. Volume, percent free air space and weight of orchid seeds. (a) Volume is calculated as $2(\pi/3r^2h)$. Except in very light seeds volume increases with weight. (b) Percent air space is given as $((\text{seed volume} - \text{embryo volume})/\text{seed volume}) \times 100$. This increases with seed volume. There are 119 data points in this plot. (c) Seed volume vs embryo volume. There are 123 data points in this plot. The lines were generated with SigmaPlot® (SPSS Inc., Chicago, IL, USA).

Dactylorhiza (Fig. 1a; Tables 2, 3); *Goodyera* (Fig. 1b,c; Tables 1–3); *Ionopsis utricularioides* (Montalvo & Ackerman, 1987); *Ophrys* (Fig. 1c; Table 3); *Orchis* (Fig. 1a,c; Tables 1–3); *Platanthera* (Fig. 1c;

Tables 1–3); *Serapias* (Fig. 2) in Europe (Neiland & Wilcock, 1995); and other orchids (Ackerman & Zimmerman, 1994). Pollen load may be a determinant in the case of *Calypso bulbosa* var. *americana*,

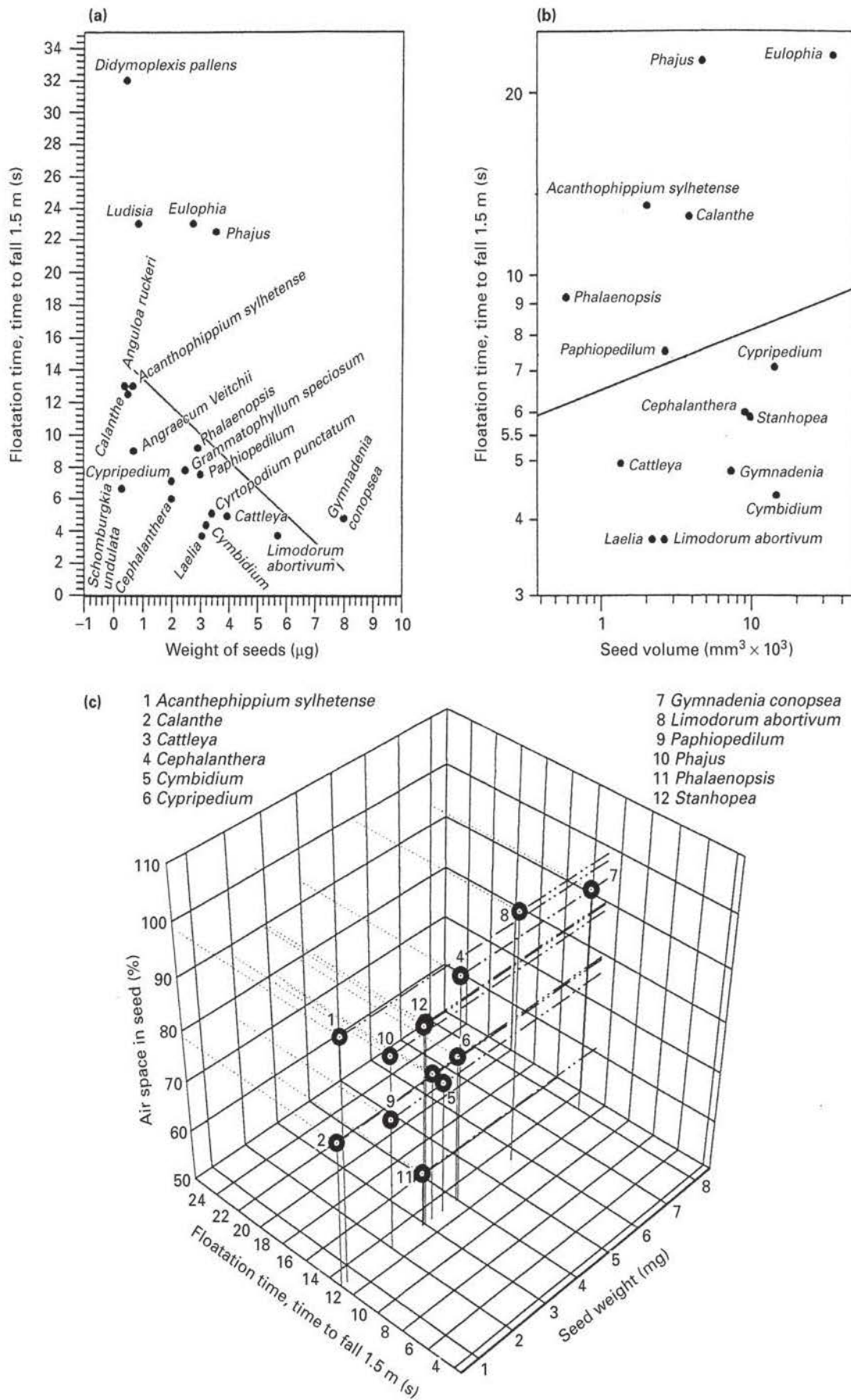


Fig. 6. Floatation in air of orchid seeds. (a) Seed weight vs floatation. With a few exceptions heavier seeds float for shorter periods. Mean weight of seeds $2.873 \mu\text{g}$ (SD 2.17); mean floatation time 9.973 s (SD 7.64). (b) Seed volume vs. floatation. Larger volumes increase floatation time. (c) Floatation vs seed weight and percent air space. Larger seed volumes and smaller weights increase floatation time. Lines generated with SigmaPlot®.

but not *Cypripedium* (Figs 3, 7; Tables 1, 2), and *Amerorchis* (*Orchis*) *rotundifolia* (Table 3; Proctor & Harder, 1994). Unknown and/or compatibility factors may also be involved because one third of hand-pollinated flowers of *Ionopsis utricularis* (*utricaroides*) failed to set fruits in field experiments in Puerto Rico (Montalvo & Ackerman, 1987), and additional pollination could not augment fruit production in *Oeceoclades maculata* (Table 2; Gonzales-Diaz & Ackerman, 1988).

Resource limitations and prior fruiting play a major role in reduced fruit and seed set in orchids. Fruit and seed production during one year can reduce growth, number of flowers, fruit set and seed numbers during the following season (Montalvo & Ackerman, 1987; Snow & Whigham, 1989; Zimmerman & Aide, 1989; Ackerman & Zimmerman, 1994). This occurs in *Aspasia principissa* (Zimmerman & Aide, 1989). Fruit set itself may be a limiting factor in *Cypripedium* (Figs 3, 7; Tables 1, 2; Nilsson, 1979). For example, fruiting by 3500 flowers of *Cypripedium calceolus* (Figs 3, 7; Tables 1, 2) in eight Estonian populations over 11 yr was 10.5% (Kull, 1998). Fruit set by the neotropical *Brassavola nodosa* (Table 3) was 30% in the summer, but less during other seasons for a total of 13% over a seven month period (Murren & Ellison, 1996). On the average fruit set by nectarless and nectariferous orchids in North America is 19.5% and 49.3%, respectively. Equivalent figures are 27.7% and 63.1% for Europe, 41.4% and 74.4% in the southern temperate hemisphere, and 11.5% and 24.9% for the tropics (Neiland & Wilcock, 1998). Darwin also devoted some thought to this subject (Box 3).

III. SIZE

As already mentioned, orchid seeds are very small (Beer, 1863; Burgeff, 1936; Ziegenspeck, 1936; Poddubnaya-Arnoldi & Selezneva, 1953, 1957a,b; Arditti, 1967, 1979, 1992; Rauh *et al.*, 1975; Arditti *et al.*, 1982; Arditti & Ernst, 1984; Rasmussen, 1995; Figs 1–4; Tables 1, 2). Variability in size is considerable in the family, in genera and even within species. The longest seed (6.0 mm), that of the neotropic *Epidendrum secundum* type is 120 times longer than the shortest (0.05), which is produced by the New Caledonian *Anoetochilus imitans* (Hallé, 1977). Note that *Epidendrum secundum* was or could be assigned to three different genera – such taxonomic convolutions are common in orchids. Hence this orchid was known as *Stenocoryne secunda*, but could also be *Bifrenaria secunda* because Rudolph Schlechter (1872–1925) as well as more recent taxonomists consider *Stenocoryne* to be a synonym of *Bifrenaria*.

Other long seeds are those of: *Lecanorchis japonica* (4.28 mm; Table 1; Kim *et al.*, 1979); *Epidendrum*

ibaguense (2.9 mm; Jordão *et al.*, 1988); *Galeola nudifolia* (3.1 mm; Table 1; Barthlott & Ziegler, 1981); and *Dendrobium insigne* (2.47 mm; Benzing & Clements, 1991).

Very short seeds are produced by: *Anoetochilus imitans* (0.050 mm; Hallé, 1977); *Aplectrum hyemale* (0.110 mm; Table 3; Stoutamire, 1981); *Dichaea* (0.120 mm; Barthlott & Ziegler, 1981); *Earina valida* (0.150–0.200 mm; Hallé, 1977); *Liparis elliptica* (0.150 mm; Hallé, 1977); several *Phraetia* (Table 1) spp. (0.120–0.170 mm; Hallé, 1977); *Schoenorchis micrantha* (0.150 mm; Hallé, 1977); and *Vanilla planifolia* (Figs 1b, 2; Table 1), although seed length in this species may vary between 0.133 and 0.300 mm (Bouriquet, 1947).

Among the 'widest' seeds are those of *Dendrobium insigne* (0.9 mm; Benzing & Clements, 1991) and *Galeola nudifolia* (0.93 mm; Table 1; Barthlott & Ziegler, 1981). They are 90 times 'wider' than the 'thinnest' ones, those of the *Gastrodia* type (Fig. 1c; Dressler, 1993), which measure 0.01–0.1 mm. (Since orchid seeds are actually tubular, 'wide' and 'thin' are terms of convenience that refer to diameter, which is technically very difficult to measure.)

Other orchids which produce slender seeds include terrestrial species (0.07–0.4 mm; Tables 1, 2; Rasmussen, 1995; the assertion by Rasmussen that seeds of epiphytic species are 'smaller' than those of terrestrial ones is incorrect). These include: *Acanthephippium* (sometimes spelled *Acanthophippium*) *sylhetense* (Fig. 2, Tables 1, 4; 0.07 mm; Burgeff, 1936); *Cattleya aurantiaca* (Table 3; 0.08 mm; Arditti, 1992); *Chiloschista lunifera* (0.05 mm; Barthlott & Ziegler, 1980); *Dendrobium nobile* (Tables 1, 3; 0.08 mm; Ito, 1955); *Goodyera pubescens* (Fig. 1c, Tables 1,3; 0.08–0.1 mm; Curtiss, 1893; Arditti, 1992); *Haemaria discolor* (now *Ludisia discolor*); 0.09 mm; Figs 1b, 2, Table 3; Burgeff, 1936); *Hormidium coriaceum* (0.09 mm; Jordão *et al.*, 1988); *Leochilus scriptus* (0.05 mm; Chase & Phippen, 1988); *Lockhartia oerstedii* (0.075 mm; Chase & Phippen, 1988); *Maxillaria rufescens* (0.075 mm; Chase & Phippen, 1988); *Miltonia spectabilis* (0.062 mm; Chase & Phippen, 1988); *Mormolyca ringens* (0.034 mm; Chase & Phippen, 1988); *Orchis anatolica* (0.027 mm; Tables 1,4; Wildhaber, 1972); *Pachyphyllum muscoides* (0.075 mm; Chase & Phippen, 1988); *Phalaenopsis* (0.075–0.96 mm; Tables 1, 3; Linder, 1930; Bernard, 1937); *Thunia marshalliana* (0.091 mm; Table 3; Henriksson, 1951); *Trichocentrum panduratum* (0.061 mm; Henriksson, 1951); *Zeuxine elongata* (0.074 mm; Table 1; Molvray & Kores, 1995).

Orchid embryos are also very small (Table 1). Some of the smallest embryos are produced by the following: *Acanthephippium sylhetense* (0.058 × 0.042 mm; Fig. 2, Tables 1, 3; Burgeff, 1936); *Pogonia triantophorus* (now *trianthophora*; 0.08 × 0.06 mm; Table 1; Curtiss, 1893); and *Vanilla planifolia*

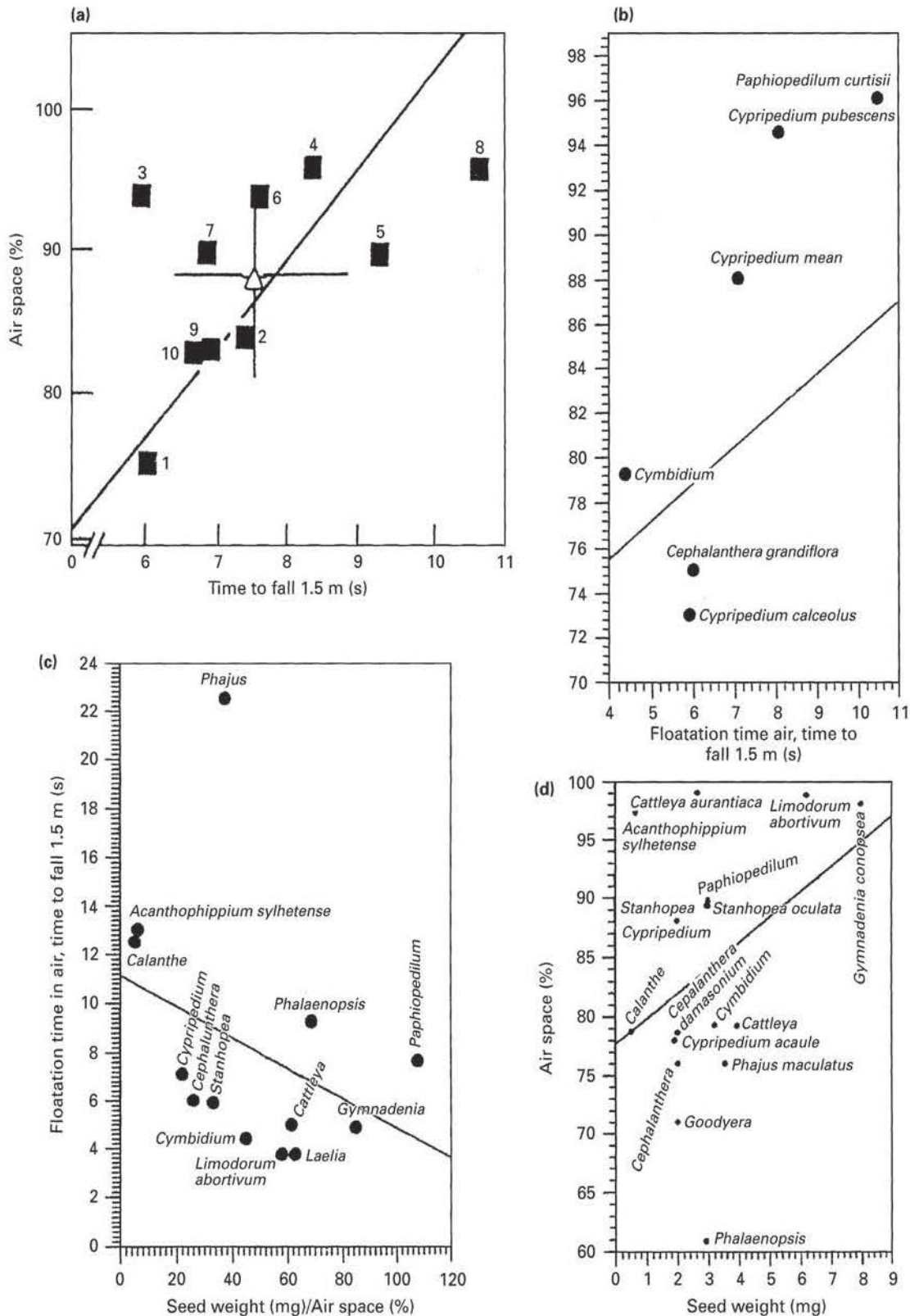


Fig. 7. Floatation of orchid seeds in air vs percent air space and weight. (a) Floatation time vs air space in seeds of California orchids (graph and statistics – Gandawijaja & Arditti (1983); floatation time – Burgeff (1936); air space – Arditti *et al.* (1979, 1980), Healey *et al.* (1980)). Nos. 1–10: 1, *Cephalanthera grandiflora* (now *Cephalanthera damasonium*: percent air space, 75; seconds to fall 1.5 m, 6.0); 2, *Corallorhiza innata* (83%, 7.2 s); 3, *Cypripedium calceolus* var. *parviflorum* (93%, 5.9 s); 4, *Cypripedium calceolus* var. *pubescens* (96%, 8.1 s); 5, *Epipactis latifolia* (now *Epipactis helleborine*: 90%, 9.1 s); 6, *Epipactis palustris* (93%, 7.5 s); 7, *Epipactis rubiginosa* (now *Epipactis atrorubens*: 90%, 6.8 s); 8, *Paphiopedilum curtisii* (now *Paphiopedilum superbiens*: 96%, 10.5 s); 9, *Platanthera bifolia* (82%, 6.8 s); 10, *Platanthera chlorantha* (82%, 6.6 s). Mean percent air space for these orchids is 88 ± 6.7 . The mean time to drop 1.5 m is 7.5 ± 1.4 s. The correlation coefficient is 0.5%. The open triangle indicates the point at which the means intersect; vertical bar is SD for percent air space; horizontal bar is SD for floatation time. (b) Floatation time of orchid seeds of similar weight with different percentages of free air space. Time of floatation increases with percent air space. Mean weights: *Paphiopedilum*

(0.1 × 0.078 mm; Fig. 1b, 2, Table 1; Bouriquet, 1947). Large or small, the great majority of orchid embryos do not have a cotyledon or an endosperm (Arditti, 1967, 1979, 1992; Arditti & Ernst, 1984).

IV. AIR SPACE IN THE SEEDS

Most orchid seeds are fusiform (Figs 1–4) and approximate two cones joined at their bases. Therefore their internal volume can be estimated with the formula:

$$2[(w/2)^2 \cdot (0.5l) \cdot (1.047)] = 2\left(\frac{\pi}{3}r^2h\right) = 2(1.047r^2h) \quad \text{Eqn 1}$$

(w , width; $(w/2)^2$, radius²; l , seed length, $0.5l$, h (eight of each cone); $\pi/3$, 1.047). The volume of relatively few orchid seeds has been calculated. It can range from $< 2.00 \text{ mm}^3 \times 1000^3$ to $40 \times 1000^3 \text{ mm}^3$ (Table 1).

Prolate spheroids (Fig. 2b) are formed by rotating an ellipse about its major axis. As even cursory inspections with dissecting microscopes indicate, orchid embryos (Figs 1, 2d) are prolate spheroids. Moreover, their longer (main or major) and biological (smaller cells at the tip, larger ones at the suspensor end) axes are one and the same. The volume of prolate spheroids (Fig. 2b) is:

$$\frac{4}{3} \pi ab^2 = 4.19ab^2 \quad \text{Eqn 2}$$

($a = 0.5 \times$ length (or major axis); $b = 0.5 \times$ width (or minor axis.) Oblate spheroids (Fig. 2b) are formed when an ellipse rotates around its minor axis. Orchid seeds are clearly not oblate spheroids despite erroneous assertions to the contrary (Stoutamire, 1981). The volume of oblate spheroids is:

$$\frac{4}{3} \pi a^2b = 4.19a^2b \quad \text{Eqn 3}$$

($a = 0.5 \times$ length (or major axis); $b = 0.5 \times$ width (or minor axis). An embryo with semi axes of $a = 0.16 \text{ mm}$ and $b = 0.1 \text{ mm}$ will have a volume of 0.670 mm^3 if treated as a prolate spheroid and only 0.107 mm^3 as an oblate one. The difference (6.26-fold in this example) is too large to ignore. Embryo volumes range from $c. 0.0001 \text{ mm}^3 \times 1000^3$ to $c. 5.0 \text{ mm}^3 \times 1000^3$ (Table 1). Note that a number of embryo volumes calculated as $4/3 \pi a^2b$ (on the erroneous

assumption that they are oblate spheroids) are inaccurate and misleading, but cannot be recalculated because the lengths of the a and b semi-axes are not given in the original source (Stoutamire, 1983).

In addition to being small, orchid seeds are also very light, with the heaviest known being produced by the Asia-Pacific genus *Galeola* (14–17 μg) and the lightest coming from the South American *Anguloa* (0.3–0.4 μg). The ratio between the lightest and highest known weights is $c. 40$ – 60 . Because of their large internal air space, such light seeds are very buoyant in both air and water. An estimate of this buoyancy as w/v is analogous to density. This means that heavier and larger seeds which have relatively bigger air spaces may be as or more buoyant (less 'dense') than more diminutive and lighter seeds with proportionally smaller air spaces. Also, the trend is for total seed volume (Fig. 5a) and percent air space (Fig. 7d) to increase as seeds become heavier and longer (Fig. 8a), but not necessarily wider (Fig. 8b,c).

Seed volumes do increase when embryo volumes are relatively small, but they quickly reach a plateau and further increases, although large, are limited to a few seeds (Fig. 5c). These observations (Figs. 5, 7a, 8a) suggest that embryos may become heavier and/or larger as seeds grow bigger and roomier, but the increases may not be directly proportional to seed volume. Given the large number of orchid species and the paucity of information (i.e. limited number of data points in the graphs, the largest being 123, in Fig. 5c, which is only a small fraction of the 25 000–30 000 orchid species) the generalizations presented here should be treated with caution. They may change as more information becomes available, but with the extent and direction of orchid research being what it is at present not much can be expected in the near future.

Free air space in seeds is variable (Tables 1,3). At 8.2%, the free air space in *Dactylorhiza foliosa* is among the smallest, whereas the largest is 99% in *Cattleya* (a ratio of 12:1). Volume : weight ratios in orchid seeds have been described as being high due to the so-called scobiform shape of the seeds, without definition of the term numerically or provision of data to support the statement (Hirt, 1906; Rasmussen, 1995). A dictionary definition of 'scobiform' is 'resembling sawdust or filings', but orchid seeds do not resemble either. Other terms which should not be used to describe orchid seeds are filing-like (*Feilspansamen*) and sawdust-like (*Säges-*

seeds, 3.0 μg ; *Cephalanthera* seeds, 2.0 μg ; *Cypripedium* seeds, 2.0 μg ; *Cymbidium* seeds, 3.2 μg . (c) Floatation time as affected by the ratio between weight and percent air space (i.e. unit weight per unit free volume). (d) Seed weight vs percent air space. The regression line is steep because some seeds have a relatively large free air space.

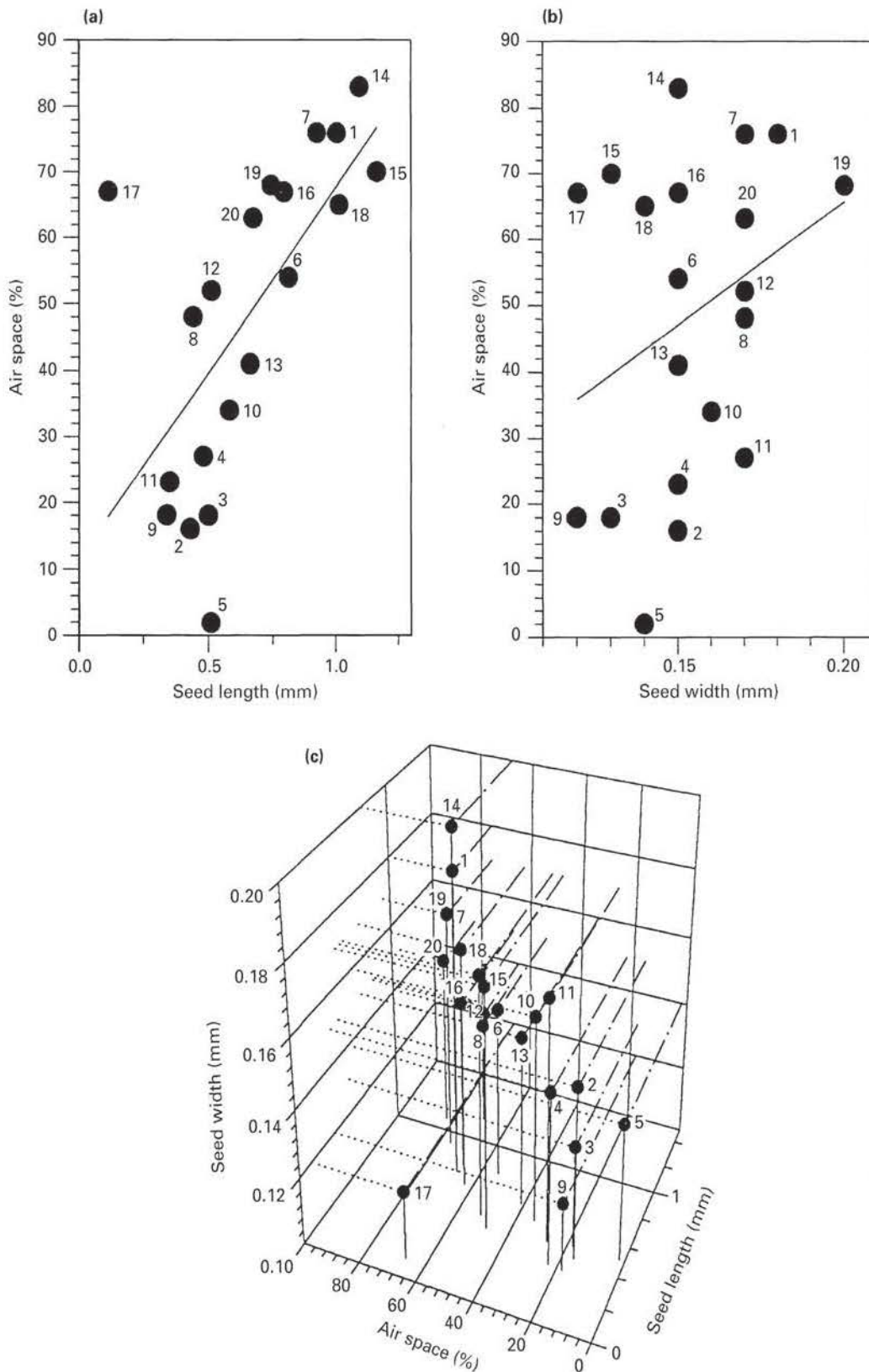


Fig. 8. Testa dimensions and percent free air space in *Paphiopedilum* seeds. (a) Length vs air space. (b) Width vs air space. (c) Percent air space vs seed width and length. Species: 1, *P. delenatii*; 2, *P. belatulum*; 3, *P. concolor*; 4, *P. godefroyae*; 5, *P. philippinense*; 6, *P. rothschildianum*; 7, *P. stonei*; 8, *P. haynaldianum*; 9, *P. lowii*; 10, *P. hisutissimum*; 11, *P. insigne*; 12, *P. fairrieianum*; 13, *P. druryi*; 14, *P. callosum*; 15, *P. ciliolare*; 16, *P. acmodontum*; 17, *P. purpuratum*; 18, *P. venustum*; 19, *P. glaucophyllum*; 20, *P. lemianum* var. *purpuratum*.

pansamen; Rauh *et al.*, 1975; Barthlott, 1976). A point to keep in mind is that dust, filings or sawdust have no internal air spaces. Furthermore, volume :

weight ratios can be high or low even in seeds or other objects that are not scobiform. Volume : weight (Fig. 5a), air space : volume (Fig. 5b) and air

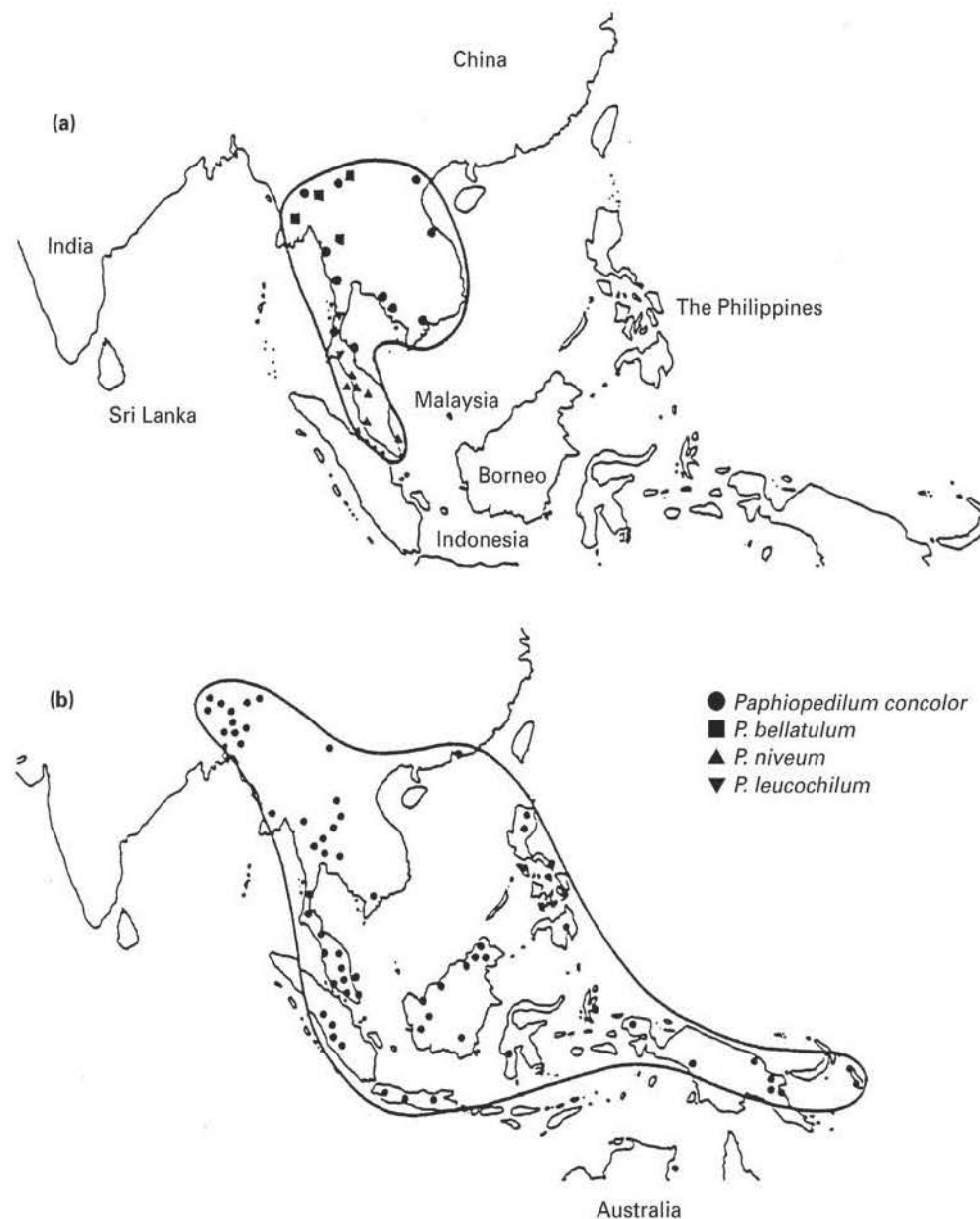


Fig. 9. Distribution of *Paphiopedilum* subgenera (a) *Brachypetalum* and (b) *Sigmatopetalum* (Karasawa & Saito, 1982).

space : weight ratios (Fig. 7d) are determined mostly by testa/embryo length (Fig. 8a,c) and to some extent width (Fig. 8b) relations, not by their shapes (Fig. 2a) and can vary considerably.

V. FLOATATION AND DISPERSAL

1. Air

(a) *Physical considerations.* Because of their small size, shape and large air space, orchid seeds can float in the air for long periods (Figs 6a–c, 7a–d; Tables 1–3). Hans Burgeff seems to have been the first to study the floatation of orchid seed in the air (Burgeff, 1936). Unfortunately very few if any studies of orchid seed floatation were carried out after Burgeff.

Therefore additional quantitative information on the subject is not available. Burgeff assumed that the ability of seeds to float in the air depended on their weight. This is true for *Didymoplexis pallens*, *Ludisia* and *Gymnadenia* (Figs 6a–c, 7c), but not for *Schomburgkia* (Fig. 6a). Heavier seeds like those of *Phaius* and to some extent *Eulophia* float for longer than the lighter ones of *Cephalanthera* and *Laelia*, for example (Figs 6a–c, 7c). Seed volume (Fig. 6b) and the percentage of free air space inside the seeds (Fig. 7a,b) seem to be more important as factors that affect and perhaps even determine floatation time in air (Tables 1, 3, 4). This is clearly the case with *Paphiopedilum curtissii* seeds, which are heavier than those of *Cypripedium calceolus* var. *pubescens* (*Cypripedium pubescens*) but have a higher percentage of air space and float longer (Fig. 7b). *Cymbidium* seeds

Table 1. Physical characteristics of some orchid seeds

Orchid	Dimensions						Free air space in testa (%)	Weight (μg)
	Seed			Embryo				
	Length (mm)	Width (mm)	Volume (mm^3)	Length (mm)	Width (mm)	Volume (mm^3)		
<i>Acanthephippium</i>	1.61 ± 0.36							
<i>Acianthus</i>	1.01 ± 0.49							
<i>Anacamptys</i>	0.4 ± 0.01							
<i>Bletilla</i>	0.43 ± 0.29	0.18 ± 0.06		0.27 ± 0.12	0.12 ± 0.05			
<i>Bletilla striata</i>	0.19 ± 0.07							
<i>Bulbophyllum</i>	0.37 ± 0.19	0.2 ± 0.10	5.90 ± 4.88	0.32 ± 0.08	0.2 ± 0.11			
<i>Calanthe</i>	0.77 ± 0.21	0.14 ± 0.25	3.81 ± 0.94	0.14 ± 0.02	0.09 ± 0.02	0.87 ± 0.57	77.67 ± 8.28	
<i>Calopogon</i>		0.72 ± 0.03						
<i>Calypso bulbosa*</i>	0.8 ± 0.4	0.14 ± 0.01	2.5 ± 0.66	0.14 ± 0.02	0.08 ± 0.01			
<i>Catasetum</i>		0.45 ± 0.09	0.12 ± 0.02	1.7				
<i>Cattleya</i>	0.70 ± 0.29	0.16 ± 0.18	1.25 ± 0.99	0.12 ± 0.11				
<i>Cephalanthera damasonium</i>	0.94 ± 0.2	0.23 ± 0.04	13.1 ± 5.1					
<i>Corallorhiza</i>	0.90 ± 0.44	0.18 ± 0.04	8.80 ± 2.28	0.24 ± 0.23	0.11 ± 0.02	5.85 ± 4.02	79 ± 6.75	
<i>Cryptostylis</i>	0.63 ± 0.26							
<i>Cymbidium</i>	0.94 ± 0.33	0.22 ± 0.08	14.68 ± 4.73	0.25 ± 0.06	0.15 ± 0.05			3.2 ± 1.63
<i>Cypripedium</i>	1.07 ± 0.43	0.24 ± 0.06	14.68 ± 4.73	0.25 ± 0.06	0.34 ± 0.42	3.53	68	1.97 ± 0.06
<i>Cypripedium acaule</i>	1.53 ± 0.06	0.21 ± 0.04	23	0.26 ± 0.01	0.18 ± 0.02	4.9	78	
<i>Cypripedium calceolus</i>	0.94 ± 0.29	0.2 ± 0.03	8.73 ± 4.98	1.61 ± 0.69				
<i>Cypripedium candidum</i>	0.88 ± 0.07							
<i>Cypripedium parviflorum</i> var. <i>pubescens</i> †	1.19 ± 0.17							
<i>Cypripedium reginae</i>	1.16 ± 0.26	0.3 ± 0.04	21.16 ± 1.45	0.23 ± 0.03	0.15 ± 0.03	2.8	87	
<i>Dactylorhiza</i>	0.78 ± 0.15	0.28 ± 0.08	14.96 ± 6.27	0.26 ± 0.04	0.78 ± 0.02	4.18 ± 1.63	71.02 ± 15.48	
<i>Dactylorhiza</i>				0.23 ± 0.04	0.15 ± 0.03	0.45	93	
<i>Dendrobium</i>	0.66 ± 0.86	0.22 ± 0.34	0.53 ± 0.04	0.29 ± 0.34	0.19 ± 0.27			
<i>Dendrobium nobile</i>	0.33 ± 0.09	0.08 ± 0.02						
Tribe Disae	0.43	0.16						
<i>Disa</i>	0.31 ± 0.3	0.26 ± 0.18						
<i>Disa</i> , Group 1	0.32	0.14						
<i>Disa</i> , Group 2	1.09	0.52						
Tribe Epidendreae	0.18–3.85							
<i>Epidendrum</i>	1.31 ± 1.41							6
<i>Epipactis</i>	1.16 ± 0.38	0.25 ± 0.07	21.94 ± 8.14	0.19 ± 0.01	0.15 ± 0.05	1.46	89.62 ± 2.6	
<i>Epipactis atrorubens</i>	0.9 ± 0.06	0.29 ± 0.02	19.28 ± 3.28				85	
<i>Epipactis gigantea</i>	0.17 ± 0.17	0.28 ± 0.13	38.17 ± 2.71				88	
<i>Epipactis helleborine</i> ‡	1.15 ± 0.15	0.25 ± 0.02	18.23 ± 4.34				92	
<i>Epipactis latifolia</i>	1.19 ± 0.18	0.21 ± 0.02	14 ± 1.1				90	
<i>Epipactis palustris</i>	1.38 ± 0.42	0.26 ± 0.08	25.81 ± 5.25	0.22 ± 0.05	0.4 ± 0.02		92	
<i>Epipactis rubiginosa</i> §							90	
<i>Epipogium</i>	0.34 ± 0.21							

<i>Galeola</i>	1.25±0.97	0.79±0.22	434					18.33±5.13	
<i>Geodorum</i>	1.3±0.49								
<i>Goodyera</i>	0.98±0.37	0.12±0.03	4±1.39	0.2±0.05	0.09±0.02	0.78±14		71.42±9.07	
<i>Goodyera oblongifolia</i>	0.96±0.07	0.13±0.02	4.1±1.3					77	
<i>Goodyera pubescens</i>	2.5±1.9	0.1±0.01	2.5±0.5	0.22±0.08	0.25±0.35	0.73±0.07		63.04±5.13	
<i>Goodyera repens</i>	0.73±0.23	0.14±0.03	4.15±1.3	0.19±0.04	0.09±0.02	0.72		82	
<i>Gymnadenia</i>	0.62±0.14							98	8
<i>Habenaria</i>	0.84±0.62	0.26±0.16	3.83	0.26±0.16	0.16±0.09	2.02		47	
<i>Hataeria</i>	1.47±0.17	0.09±0.01							
<i>Lecanorchis</i>	3.38±0.67	0.13±0.03	15.07±2.88						
<i>Limodorum abortivum</i>	0.78±0.63	0.29±0.23	81	0.04	0.02				5.7
<i>Liparis</i>	0.49±0.26	0.15±0.02	3.43±3.1	0.15±0.07	0.11±0.05	0.86±0.87		67.99±32.49	
<i>Listera cordata</i>	0.69±0.17	0.19±0.07							
<i>Listera ovata</i>	0.77±0.16	0.22±0.01	9.7±2.46						
<i>Malaxis</i>	0.39±0.1								
<i>Microtatorchis</i>	0.48±0.10								
<i>Monadenia</i>	0.28±0.08	0.13±0.02							
<i>Neottia</i>	0.88±0.15	0.28±0.09	21.68±5.99						
<i>Neottia nidus-avis</i>	0.90±0.15	0.27±0.09	22.67±5.41						
<i>Nevillia</i>	0.29±0.07								
<i>Neuwedia</i>	0.66±0.25	0.26±0.07	38						
<i>Nigritella</i>	0.36±0.03	0.19±0.02	3.67	0.18±0.01	0.12±0.02				
<i>Oberonia</i>	0.18±0.03								
<i>Odontoglossum</i>	0.42±0.05	0.1±0.02	1.14±0.40	0.24±0.11	0.09±0.01	0.6		48	
<i>Oncidium</i>	0.42±0.22	0.10±0.05	1.83±2.35						
<i>Ophrys</i>	0.50±0.11	0.15±0.04	4.58±2.58	0.16±0.05	0.10±0.03				
<i>Orchis</i>	0.49±0.17	0.17±0.06	3.93±3.24	0.18±0.05	0.12±0.04	1.22±0.77		43.01±35.16	
<i>Orchis coriophora</i>	0.46±0.06	0.18±0.05	4.17±2.7	0.2±0.02	0.14±0.2	1.11		77	
<i>Orchis mascula</i>	0.39±0.13	0.18±0.03	6.43±3.98	0.21±0.1	0.14±0.01	1.64		71	
<i>Orchis morio</i>	0.56±0.16	0.18±0.05	5.73±4.52	0.18±0.04	0.12±0.03	1.35±0.13		76.05±12.87	
<i>Orchis purpurea</i>	0.38±0.04	0.15±0.07	2.65±1.69	0.15±0.03	0.09±0.03	0.78±0.34			
<i>Orchis saccata</i>	0.52±0.01	0.13±0.05	2.9±1.5	0.14±0.03	0.11±0.01	1.72		58	
<i>Orchis simia</i>	0.38±0.09	0.15±0.08	4.2	0.16±0.03	0.11±0.03	1.55		73	
<i>Paphiopedilum</i>	0.7±0.35	0.15±0.04	4.36±2.06	0.23±0.05	0.124±0.03	1.78±0.66		62.38±21.08	
<i>Paphiopedilum barbatum</i>	0.6±0.43	0.10±0	1.6±1.21						
<i>Paphiopedilum insigne</i>		0.17±0.05							
<i>Phaius</i>	0.96±0.18								
<i>Phalaenopsis</i>	0.35±0.05	0.08±0.01	0.59±0.34	0.20±0.05	0.08±0.01			53	2.91
<i>Phreatia</i>	0.15±0.03								
<i>Piperia</i>	0.54±0.1	0.18±0.04	4.69±1.84	0.18±0.03	0.11±0.03	0.53±0.66		75±10.33	
<i>Platanthera</i>	0.64±0.20	0.25±0.04	13.13±4.54	0.25±0.05	0.16±0.03	2.38±0.6		81.21±3.27	
<i>Pogonia</i>	1.04±0.27	0.18±0.01	8.73±2.11	0.18±0.09	0.1±0.04	4.88		16	
<i>Ponerorchis</i>	0.39±0.02	0.19±0.01	3.57±0.26	0.21±0.04	0.16±0.04				
<i>Pterostylis</i>	0.66±0.33								
<i>Sarcochilus</i>	0.39±0.09								

Table 1 (cont.)

Orchid	Dimensions						Free air space in testa (%)	Weight (µg)
	Seed			Embryo				
	Length (mm)	Width (mm)	Volume (mm ³)	Length (mm)	Width (mm)	Volume (mm ³)		
<i>Satyrium</i>	0.39±0.06	0.14±0.02	2.64	0.21±0.08	0.09±0.03			
<i>Schizochilus</i>	0.28±0.05	0.22±0.04						
<i>Spathoglottis</i>	10.09±0.21	0.30±0.04	22.13±9.95	0.26±0.06	0.14±0.03	5.69	72	
<i>Spiranthes</i>	0.51±0.16	0.13±0.03	3.1±3.78	0.18±0.05	0.10±0.05		69	
<i>Stanhopea</i>	0.39±0.25	0.28±0.17		0.17±0.13	0.09±0.06			
<i>Taeniophyllum</i>	0.34±0.11							
<i>Thelymitra</i>	0.31±0.06							
<i>Vanda</i>	0.31±0.13							
<i>Vanilla</i>	0.25±0.08	0.22±0.06	2.87±2.71					
<i>Zeuxine</i>	1.23±0.52	0.1±0.01						

There are few published systematic, statistical and/or morphometric studies of orchid seeds. Information of the kind presented in this table must be compiled from numerous sources that vary in accuracy and reliability; report on seeds from natural populations or plants that were apparently cultivated under different and usually not fully described conditions; probably refer to seeds and fruits in various stages of development and maturation; span more than 100 years; and are in many languages. A number of the values were obtained by measuring illustrations (drawings, light photographs and SEM micrographs). Even after a wide literature search only partial information is available for most genera and species.

To allow for useful statistical parameters (mean ± SD, as shown), calculations were limited to genera and species for which there were at least three data points. Averages based on one or two data points, and therefore without SD, are included in some instances to provide a more complete picture. Percent free air space in the testa was calculated as: ((seed volume - embryo volume)/seed volume) × 100. Seeds were assumed to be two cones joined at their bases and their volume was estimated as $2((\text{width}/2)^2 \times (\text{length}/2) \times 1.047)$. Embryos were assumed to be prolate spheroids and their volume was approximated as $\frac{4}{3}\pi ab^2$ (a = length/2; b = width/2). Measurements or calculations (i.e. volume) are inaccurate or wrongly calculated in several previous reports (for example when orchid embryos were treated as oblate spheroids by Stoutamire (1981)). When errors were obvious the data were not used to make calculations. Further, the limited amount of available information precluded statistical calculations that could reflect the frequency and distributions of dimensions (for example, determine if certain seed length(s) are predominant, common or rare within a genus); that such differences do occur is obvious from the *Disa* entries. Calculations that were possible with the available data imply equal and uniform distribution of dimensions within genera and species.

Orchid nomenclature and taxonomy are very fluid - nomenclatural and classification changes of taxa are common. Since this table contains many orchid names, a determination of currently 'valid' taxonomic concepts would require a nomenclatural study of the entire family, and thus all names used here are the ones that appear in the original sources, except as indicated. The sources are: Link, 1839-1842; Beer, 1863; Beccari, 1877; Anonymous, 1879; Curtiss, 1893; von Marilaun, 1896; Bernard, 1909, 1937; Schlechter, 1915; Knudson, 1921, 1922; Ames, 1922a,b, 1948; Fleischer, 1929, 1930; Linder, 1930; Quednow, 1930; Curtis, 1932; Francini, 1932; Gratiot, 1934; Burgeff, 1936; Carlson, 1936; Ziegenspeck, 1936; Hoene, 1945; Davis, 1946; Maheshwari & Narayanaswami, 1952; Poddubnaya-Arnoldi & Selezneva, 1953, 1957a,b; Ito, 1955; Scott & Arditti, 1959; Leuschner, 1960; Kupper & Linsenmaier, 1961; Zimmerman & Dougoud, 1961; Hey, 1962; Mitsuura *et al.*, 1962; Nakamura, 1962, 1964; Hamada & Nakamura, 1963; Stoutamire, 1964a,b, 1983; Rauh *et al.*, 1965; Hey & Hey, 1966; Zinger & Poddubnaya-Arnoldi, 1966; Clifford & Smith, 1969; de Vogel, 1969; Fuller, 1969a,b, 1970a, 1972, 1981; Veyret, 1969; Voth, 1959, 1963, 1964, 1969; Fuller, 1969, 1970b; Vanseveren-Van Espen, 1971; Wildhaber, 1969, 1970, 1972, 1974; Harvais, 1973; Leuchs, 1973; Barthlott, 1974, 1976; Rauh *et al.*, 1975; Haas, 1977; Hallé, 1977; Chua & Rao, 1978; Hasegawa *et al.*, 1978; Jordão *et al.*, 1988; Arditti *et al.*, 1979, 1980; Kim *et al.*, 1979; Mohana *et al.*, 1979; Healey *et al.*, 1980; Sheviak & Bye, 1980; Dafni, 1981; Barthlott & Ziegler, 1981; Lucke, 1981, 1982a,b, 1983, 1984a,b; Arditti, 1992; Karasawa & Saito, 1982; Gandawijaja & Arditti, 1983; Tohda, 1983, 1985, 1986; Cherevchenko & Kushnir, 1986; Chase & Pippen, 1988, 1990; Singh, 1981; Sood, 1989; Benzing & Clements, 1991; Petersson, 1991; Stewart, 1992; Kurzweil, 1994; Dressler, 1993; Proctor & Harder, 1994; Raghavan & Goh, 1984; Shoushtari *et al.*, 1994; Wagner & Hansel, 1994; Zettler & McInnis, 1994; Molvray & Kores, 1995; Rasmussen, 1995; Vij *et al.*, 1995; L. C. Wheeler, pers. comm.

*This is a monotypic genus.

†*Cypripedium pubescens* is another name for this *Cypripedium* species.

‡This species is also known as *Epipactis helleborine* var. *helleborine*.

§Another name for this species is *Epipactis atrorubens* var. *atrorubens*.

||It is not uncommon to see this name spelled as *Phajus*.

that weigh not much more than those of *Paphiopedilum* but have considerably less air space float for much shorter periods (Fig. 7b). Also, seeds of *Cephalanthera damasonium* (*Cephalanthera grandiflora*) and *Cypripedium calceolus* (which are of equal weight, but have a smaller proportion of free air space than *Cymbidium*) float for an even shorter time (Fig. 7b).

Within the genus *Paphiopedilum* (Ando & Tomiyama, 1990), the percentage of air space seems to increase more in proportion to seed length (Fig. 8a,c) than width (Fig. 8b). As a consequence the longer seeds of subgenus *Sigmatopetalum* (some taxonomists consider this group to be section *Barbata* in the subfamily *Paphiopedilum*) have larger air spaces (Fig. 8a-c) and float for longer periods (Table 3; Karasawa & Saito, 1982). For example, floatation time for seeds of a hybrid with *Paphiopedilum callosum* (seed length, 1.09 mm; width, 0.15; air space, 83%) as the seed parent is 9.6 s (to fall 1.5 m). By contrast, seeds produced by a cross with *Paphiopedilum insigne* (length, 0.48 mm; width, 0.17 mm; air space, 27%) as the seed parent floated for only 4.2 s (Burgeff, 1936; Karasawa & Saito, 1982).

Floatation time is inversely proportional to the seed weight : percent air space ratio (Fig. 7c). This ratio becomes smaller as percent air space (the divisor) becomes larger (i.e. mass per unit of air space or a property which can be equated to density decreases). Altogether it is clear that weight probably plays a less important role in floatation time than percent (i.e. free) air space inside the seeds and seed volume.

To measure floatation time, Burgeff dropped seeds through a glass cylinder (1.5 m long, 40 mm diameter) which was placed over a 50 mm (presumably diameter) white or black glass plate (Burgeff, 1936). He timed the fall with a stop watch. His measurements are still the only ones available and because of that they are referred to often. Burgeff was generally a careful worker and a good technician, but not necessarily a good theoretician (as indicated by his *Orcheomyces* classification for mycorrhizal fungi isolated from orchids (Burgeff, 1909, 1911, 1932, 1936) and his failure to develop asymbiotic germination of orchid seeds). Lewis Knudson (1884–1958) of Cornell University developed the asymbiotic method for orchid seed germination in his very first reported experiment with orchids (see Arditti, 1990), when Burgeff had been working on seed germination and mycorrhizae of orchids for c. 15 yr.

There is no doubt that Burgeff's measurements are accurate as they stand, but they are not representative of what may happen under natural conditions because the air in his glass tube and laboratory was probably still and the seeds simply fell down due to gravity. Under natural conditions air is seldom still. Seeds which are released into the

air may float for a while and start to descend, but they can be (and most probably are) repeatedly blown in all directions by air turbulence and winds of varying intensities. Seeds with larger air spaces and longer vertical floatation times in Burgeff's tube may be affected differently by wind and turbulence than those that are smaller, less 'dense' and/or drop faster. As a result, floatation times of seeds in their natural habitats are undoubtedly different and more varied than in the laboratory and their trajectory is almost certainly not vertically down in a nearly straight line as it must have been in Burgeff's cylinder. Consequently, his measurements and data should be viewed only as approximations and indications of time periods during which the seeds can be affected by air currents.

More realistic information and experimental results about the floatation and travel distance is available in two illuminating and interesting recent reports that describe well-designed and clever experiments (Carey, 1998; Murren & Ellison, 1998). In addition to the intrinsic value of each report, the two when taken together have an added value because one deals with a tropical epiphyte and the other with a European terrestrial species.

(b) *Dispersal*. Orchid seeds can be assumed to be very small and very light balloons. In fact, the seeds of the following, for example, even look like balloons: *Epipogium nutans* (Fig. 2d; current name *Epipogium roseum*); *Epistephium parviflorum* (Fig. 1b); *Eulophia streptopetala* (Fig. 1b); *Gongora maculata* var. *pallida* (Fig. 1b); *Haematorchis altissima* (Fig. 1b); *Listera australis* (Fig. 2d); *Listera convallarioides* (Fig. 2d); *Neottia nidus-avis* (Fig. 1a); *Pleione formosana* (Fig. 2d, now *Pleione bulbocodioides*); *Schizochilus zeyheri* (Fig. 2d); *Stanhopea insignis* (Fig. 1b); *Stanhopea oculata* (Fig. 1b, 2d); *Stanhopea oculata* (Fig. 1b, 2d); *Stanhopea saccata* (Fig. 2d); *Stanhopea tigrina* (Fig. 1a, 2d); *Vanilla planifolia* (Fig. 1b, 2d), and *Zygopetalum intermedium* (Fig. 2d).

One of the two recent reports (Murren & Ellison, 1998; A. E. Ellison, pers. comm.) describes well thought out and interesting experiments with seeds of the Central American orchid *Brasavola nodosa* (also known as *Dama de la Noche*, or Lady of the Night, because it becomes fragrant in the evening). Their shape is similar to those of *Brasavola cordata*, Fig. 1c; they measure $640 \pm 40.6 \times 56 \pm 4.8 \mu\text{m}$, and weigh $1.6 \mu\text{g}$. This report provides theoretical, physical and mathematical underpinnings for considerations of floatation, flight and dispersal of orchid seeds (Murren & Ellison, 1998; A. E. Ellison, pers. comm.). Starting with the assumption that wind dispersal of orchid seeds may be similar to a ballistic model proposed for *Eucalyptus* and described by the equation:

$$X_m = h \frac{U_c}{U_t} \quad \text{Eqn 4}$$

Table 2. *Orchid seeds : numbers and weights*

Species	Seeds (capsule ⁻¹ , mg ⁻¹ , fruit ⁻¹ , or µg seed ⁻¹)			Refs
	Weight	Number	Plant ⁻¹	
<i>Acropera (Gongora)</i>		3712577	4000000	Darwin, 1904
<i>Anacamptis pyramidalis</i>		1935	35000	Tournay, 1960*
<i>Anguloa clowesii</i>	1100 seeds mg ⁻¹ 0.91 µg seed ⁻¹			Cherevchenko & Kushnir, 1986
<i>Anguloa ruckeri</i>		3932948		Thomale, 1954
<i>Anguloa ruckeri</i>	2564 seeds mg ⁻¹			Cherevchenko & Kushnir, 1986
<i>Anguloa ruckeri</i>	1524 mg fruit ⁻¹			Arditti, 1992
<i>Anguloa ruckeri</i>	0.39 µg seed ⁻¹			"
<i>Calanthe</i>	25–100 mg fruit ⁻¹			Cherevchenko & Kushnir, 1986
<i>Calanthe vestita</i>	2000 seeds mg ⁻¹ 0.5 µg seed ⁻¹			Cherevchenko & Kushnir, 1986
<i>Calypso bulbosa</i>		6800		Wildhaber, 1974
<i>Calypso bulbosa</i>				Proctor & Harder, 1994
Seeds with embryos				
Half pollinium		4909		
One pollinium		10980		
Two pollinia		15720		
<i>Cattleya</i>		Millions		Malguth, 1901, citing F. Cohn & E. Pfitzer.
<i>Cattleya</i>		500000–6000000		Poddubnaya-Arnoldi & Selezneva, 1957
<i>Cattleya aurantiaca</i>		256000		Knudson, 1956; Lenz & Wimber, 1956; Tournay, 1960*
<i>Cattleya bowringiana</i>	330 seeds mg ⁻¹ 3.03 mg seed ⁻¹			Arditti, 1992
<i>Cattleya gigas</i>		500000–700000		Cherevchenko & Kushnir, 1986
<i>Cattleya guttata</i>	870 seeds mg ⁻¹ 1.15 µg seed ⁻¹			Arditti, 1992
<i>Cattleya labiata</i>		2000000–3000000 (929000 viable)		Cherevchenko & Kushnir, 1986
<i>Cattleya labiata</i>	400 seeds mg ⁻¹			Arditti, 1992
<i>Cattleya labiata</i>	2323 fruit ⁻¹			
<i>Cattleya labiata</i>	2.5 µg seed ⁻¹			
<i>Cephalanthera damasonium</i> †		6020	24000	Tournay, 1960*
<i>Cephalanthera grandiflora</i> †		6020	24080	Darwin, 1904; Lenz & Wimber, 1959
<i>Coeloglossum viride</i>		1330	12000	Lenz & Wimber, 1959; Tournay, 1960*
<i>Cynoches chlorochilon</i>	3770000 fruit ⁻¹	3770000	3770000	Ames, 1946; Lenz & Wimber, 1959; Tournay, 1960*; estimate by Rolfe, 1912
<i>Cynoches chlorochilon</i>		3751000		Bechtel <i>et al.</i> , 1986
<i>Cynoches chlorochilon</i>		3932948		"
<i>Cynoches chlorochilon</i>	14400 seeds mg ⁻¹	4000000		Arditti, 1992
<i>Cynoches chlorochilon</i>	3.6 µg seed ⁻¹	4000000		"
<i>Cymbidium</i>	300–700 mg fruit ⁻¹			Cherevchenko & Kushnir, 1986
<i>Cymbidium</i>		1500000		Arditti, 1992
<i>Cymbidium</i> hybrid	730 seeds mg ⁻¹ 1.37 mg seed ⁻¹			Cherevchenko & Kushnir, 1986
<i>Cymbidium traceyanum</i>		850000		Weiss, 1916; Arditti, 1982
<i>Cypripedium acaule</i>		14000–54180		Tournay, 1960*
<i>Cypripedium acaule</i>		28160	28160	
<i>Cypripedium acaule</i>	526 mg ⁻¹	54180		Stoutamire, 1964b
<i>Cypripedium acaule</i>	108 mg fruit ⁻¹			Arditti, 1992
<i>Cypripedium acaule</i>	2 µg seed ⁻¹			"
<i>Cypripedium calceolus</i>				Proctor & Harder, 1994
Seeds with embryos				
Natural pollination		1435		
Quarter anther		1867		
Half anther		3660		
One anther		3158		
<i>Dactylorhiza (Dactylorhiza) fuchsii</i>		6200	186300	Tournay, 1960*

Table 2 (cont.)

Species	Seeds (capsule ⁻¹ , mg ⁻¹ , fruit ⁻¹ , or µg seed ⁻¹)		Plant ⁻¹	Refs
	Weight	Number		
<i>Dactylorhiza</i> (<i>Dactylorhiza</i>) <i>fuchsii</i> (Druce) Soó		3294	> 56000	Tournay, 1960*
<i>Dendrobium</i>	Up to 500 mg fruit ⁻¹			Arditti, 1992
<i>Dendrobium antennatum</i>	200 seeds mg ⁻¹ 5 µg seed ⁻¹			Pfitzer, 1882
<i>Dendrobium antennatum</i>	177 seeds mg ⁻¹ 5.65 mg seed ⁻¹			Cherevchenko & Kushnir, 1986
<i>Dendrobium phalaenopsis</i>	1000 seeds mg ⁻¹ 1 mg seed ⁻¹			"
<i>Dendrobium phalaenopsis</i>	1120 seeds mg ⁻¹ 0.89 mg seed ⁻¹			"
<i>Epidendrum (radicans)</i>	320 seeds mg ⁻¹			"
<i>ibaguense</i>	3.13 mg seed ⁻¹			"
<i>Epidendrum (radicans)</i>	167 seeds mg ⁻¹			"
<i>ibaguense</i>	5.99 µg seed ⁻¹			"
<i>Epipactis</i> , average for several species		4500		Wildhaber, 1970
<i>Eulophia horsfallii</i>	558 seeds mg ⁻¹ 1.79 mg seed ⁻¹	204454		Tournay, 1960*
<i>Galeola altissima</i>	17 mg seed ⁻¹ 306 mg fruit ⁻¹	18000		Hamada & Nakamura, 1963; Arditti, 1992
<i>Galeola septentrionalis</i>	384 mg fruit ⁻¹ 24 µg seed ⁻¹	16000		Hamada, 1939; Nakamura, 1964; Rasmussen, 1995; Arditti, 1992
<i>Gongora</i> sp.		317250		Darwin 1904; Withner, 1959; Tournay, 1960*
<i>Gongora</i> sp.			74000000‡	Tournay, 1960*
<i>Goodyera repens</i>		1700	25500	Tournay, 1960*
<i>Goodyera repens</i>				Rasmussen, 1995
<i>Gymnadenia conopsea</i>	2 µg seed ⁻¹	2000	32000	Tournay, 1960*
<i>Himantoglossum</i>		1200	28800	Ziegenspeck, 1936
<i>Laelia purpurata</i>	760 seeds mg ⁻¹ 1.32 mg seed ⁻¹			Cherevchenko & Kushnir, 1986
<i>Leporella fimbriata</i>		5000		"
<i>Limodorum abortivum</i>	5.7 mg			Peakall <i>et al.</i> , 1987; Peakall & James, 1989
<i>Listera cordata</i>		376	2860	Rasmussen, 1995
<i>Listera ovata</i>		544	21000	Stoutamire, 1964
<i>Malaxis monophyllos</i>		1572	19490	Tournay, 1960*
<i>Maxillaria</i>		1756440	10538640	Stoutamire, 1964b
<i>Maxillaria</i>		1756440	10538640	Darwin, 1904
<i>Maxillaria</i>			< 10000000	Tournay, 1960*
<i>Oeceoclades maculata</i>				Poddubnaya-Arnoldi & Selezneva, 1957
Cultivated plants				González-Díaz & Ackerman, 1988
Control flowers		2011 seed fruit ⁻¹ 12067 per six fruits		
Self-pollinated flowers		69% fertile seeds 893 seeds fruit ⁻¹ 30346 per thirty- four fruits		
Cross-pollinated flowers		92% fertile seeds 896 seeds fruit ⁻¹ 34034 per thirty- eight fruits		
	50.7 mg fruit ⁻¹		88% fertile seeds	

Table 2 (cont.)

Species	Seeds (capsule ⁻¹ , mg ⁻¹ , fruit ⁻¹ , or µg seed ⁻¹)		Plant ⁻¹	Refs
	Weight	Number		
Self-pollinated, one pollinium		619 seeds fruit ⁻¹ 6808 per eleven fruits		González-Díaz & Ackerman, 1988
	23 mg fruit ⁻¹	93 % fertile seeds 623 seeds fruit ⁻¹		
Self-pollinated, two pollinia		6850 per eleven fruits		
	46.2 mg fruit ⁻¹	92 % fertile seeds 515 seeds fruit ⁻¹		
Flowers on plant under artificial rain		5666 per eleven fruits ⁻¹		
	27.8 mg fruit ⁻¹	99 % fertile seeds		
Plants in the field				
Control 1		870 seeds fruit ⁻¹ 24356 per twenty- eight fruits ⁻¹		
	65.8 mg fruit ⁻¹	97 % fertile seeds 511 seeds fruit ⁻¹ 28123 per fifty-five fruits		
Control 2				
	60.7 mg fruit ⁻¹	96 % fertile seeds 498 seed fruit ⁻¹ 4,483 per nine fruits ⁻¹		
Insect exclusion				
	66.3 mg fruit ⁻¹	98 % fertile seeds 6,200 10,000	40000	Tournay, 1960* Rasmussen, 1995
<i>Oncidium</i>		'Thousands'		Poddubnaya-Arnoldi & Selezneva, 1957, 1964, 1976
<i>Ophrys apifera</i>		< 6 000 000		"
Orchids		< 10 000		"
Orchids, epiphytic		6200	186300	Darwin, 1904; Lenz & Wimber, 1959
Orchids, terrestrial			56000	Lenz & Wimber, 1959
<i>Orchis maculata</i> §		> 40 000	32000	Tournay, 1960*
<i>Orchis maculata</i> §		25 000	13750	"
<i>Orchis morio</i>		20-50		George & Cooke, 1981
<i>Platanthera chlorantha</i>		Millions		Malguth, 1901 citing F. Cohn & E. Pfitzer
<i>Rhizanthella gardenri</i>				Cherevchenko & Kushnir, 1986
<i>Stanhopea</i>				"
<i>Stanhopea oculata</i>	333 seeds mg ⁻¹ 3 mg seed ⁻¹			
<i>Stanhopea tigrina</i>	600 seeds mg ⁻¹			
<i>Stanhopea tigrina</i>	1.67 mg seed ⁻¹			
Subtropical <i>Cymbidium</i>				
Hybrid	1.37 µg seed ⁻¹			
Temperate orchid sp.	9.84 ± 10.22 µg seed ⁻¹			Calculated from data in this table. Range: 24-0.5 µg seed ⁻¹ ¶
Tropical orchid spp.	< 1 µg**			Rasmussen, 1995
Tropical orchids	2.56 ± 1.76 µg seed ⁻¹			Calculated from data in this table. Range: 0.39-5.99 seed ⁻¹ ††

Table note: see facing page.

(X_m , approximate mean distance a seed will disperse; h , height of release; U_e , average wind velocity between point of release and ground; and U_t , terminal velocity (in this case $U_t = 0.157 \text{ m s}^{-1}$). They (Murren & Ellison, 1998) measured seed dispersal in the field, wind tunnel and the laboratory. Based on their experimental evidence they concluded that modal dispersal distance (i.e. floatation and movement or travel in air) of dust-like orchid seeds was predicted adequately by this ballistic model (Eqn 4) at low wind velocities and low release heights, but that it underestimated the increasing importance of turbulence at higher wind velocities and greater release heights (Murren & Ellison, 1998). On estimating the relative importance of one measure of turbulence, vertical mixing velocity (W^*) on X_m in wind tunnel experiments (i.e. floatation distance) they found that under high turbulence adding mixing velocity to the ballistic model overestimated modal seed dispersal distances (Murren & Ellison, 1998). The reasons for this can be found in the following equations:

$$\lambda = \frac{1 + \left(\frac{W^*}{2U_t}\right)^2 + \frac{W^*}{2U_t}}{1} \quad \text{Eqn 5}$$

$$\lambda \approx 1 + \frac{W^*}{2U_t} \approx l \quad \text{Eqn 6}$$

(W^* , rate at which a suspended particle would reach the ground by eddy diffusion in the absence of gravity (Murren & Ellison, 1998); λ , dimension parameter which includes the effects of W^* and U_t and represent the spread of seed around their major location). By contrast, Burgeff's seeds fell to the ground strictly due to gravity and were not affected by eddies.

In these formulas, the value of λ will increase approximately in proportion to one third the power of airspace and this should reduce terminal velocity, U_t (A. M. Ellison, pers. comm.). In general, according to Eqns 5 and 6, the consequence of larger air spaces in orchid seeds would be an increase in the effects of turbulence (because the seeds will float longer) on modal dispersal distance and increased variance. This means that increased air space may

increase floatation time yet reduce the average travel distance of a seed, but the stray seed could go a lot further (A. M. Ellison, pers. comm.). Given the large number of seeds produced by orchids, the 'stray seed' may actually be a large number in any given year and even more over longer periods.

A somewhat different approach was used in another carefully designed and illuminating study of the spread of *Himantoglossum hircinum* (Fig. 1a) in the south of England (Carey, 1998). This study tested two dispersal (i.e. floatation and air travel) models for seeds of this species. They measure $130 \times 30 \mu\text{m}$, weigh $5 \times 10^{-9} \text{ kg}$ (Carey, 1998) and are produced at 1200 fruit^{-1} or 28800 plant^{-1} (Ziegenspeck, 1935, 1936). One of these, a diffusion model, represents dispersal as a bivariate normal distribution including root-mean-square displacement (Carey, 1998):

$$Q_{(x)} = \frac{M}{\pi R^2} \exp\left(-\frac{x^2}{R^2}\right) \quad \text{Eqn 7}$$

($Q_{(x)}$, deposition density of seeds at distance x from the parent; M , number of seeds produced by parent plant; R , root-mean-square displacement for seed dispersal). This equation takes into account the number of seeds produced by a plant (M), but not their volume and/or weight. It indicates that a large M can lead to higher $Q_{(x)}$ values over short distances and probably lower ones over longer ranges and distributions (i.e. floatation periods) similar to the ones defined by Eqns 5 and 6. For *Himantoglossum hircinum* this equation is less satisfactory than another one called the tilted plume model (Carey, 1998):

$$Q_{(x)} = \left(\frac{MW_s}{HU\Gamma(1+\beta)}\right) \left(\frac{H^2\bar{U}}{(1+\alpha)\bar{A}}\right)^{1+\beta} x^{-\beta-1} \exp\left(-\frac{H^2\bar{U}}{2(1+\alpha)\bar{A}_x}\right) \quad \text{Eqn 8}$$

($Q_{(x)}$, deposition density of seeds at distance x from the parent; M , number of seeds (many in orchids); W_s , settling velocity of the seed (orchid seeds with large air spaces drop more slowly and therefore should have a lower settling velocity); H , height at

Except as noted below the names used here are those in the original literature. In most cases there are not enough reports (at least three) for the calculation of statistical parameters (mean, SD).

*Tournay (1960) contains information from several sources – hence different values for the same species.

†This species has three names and is a typical example of the unending taxonomic gyrations that plague orchid systematics. At one time it was known as *Cephalanthera pallens*. This name was reduced to synonymy under *Cephalanthera grandiflora* and *Cephalanthera damasonium*.

‡The figure 74000000 was obtained by multiplying 200 (the number of capsules found on one plant) by 317250 (the number of seeds per capsule of another specimen of this orchid).

§Another name for this species is *Dactylorhiza maculata*.

¶*Cymbidium* was excluded from these calculations because not all species are fully tropical. If it is included the values change to $8.43 \pm 9.77 \mu\text{g seed}^{-1}$.

**This figure is incorrect as is obvious from calculations based on data in this table. It appears in a book on the seeds of terrestrial orchids (Rasmussen, 1995), may therefore be accepted as being accurate and must be corrected.

††*Cymbidium* was excluded from these calculations because not all species are fully tropical. If it is included the values change to $2.49 \pm 1.73 \mu\text{g seed}^{-1}$.

Table 3. Weight, air space and floatation of some orchid seeds in air

Species	Floatation in air (s)	Weight (µg)	Air space (%)	Refs
<i>Acanthephippium sylhetense</i>	13.0	0.66	97.35†	Burgeff, 1936
<i>Angraecum</i> cv. Veitchii	9.0		0.70	"
(<i>Angraecum eburneum</i> × <i>A. sesquipedale</i>)				
<i>Anguloa ruckeri</i>	13.0		0.39	"
<i>Anguloa uniflora</i> × <i>A. ruckeri</i>	10.0			"
Anguloa mean	11.5	0.39		
<i>Calanthe sylvestris</i> * × <i>C.</i> cv. Darblayana	12.0			"
<i>Calanthe</i> cv. Veitchii		0.5		Table 1; J. Arditti & A. K. A. Ghani, unpublished
<i>Calanthe veratrifolia</i> × <i>C. vestita</i>	13.0			Burgeff, 1936
Calanthe mean	12.5	0.5	78.75†	
<i>Cattleya aurantiaca</i>	2.65	99.00		Shoushtari <i>et al.</i> , 1994; Table 2
<i>Cattleya elongata</i>		4.1		"
<i>Cattleya forbesii</i>		3.5		"
<i>Cattleya guttata</i> × <i>C. autumnalis</i>	5.0			Burgeff, 1936
<i>Cattleya guttata</i> var. <i>leopoldinae</i> ‡	5.15			Shoushtari <i>et al.</i> , 1994
<i>Cattleya harrisoniana</i>		5.71		"
<i>Cattleya harrisoniae</i> § × <i>C. gaskelliana</i>	5.2			Burgeff, 1936
<i>Cattleya intermedia</i>		2.33		Shoushtati <i>et al.</i> , 1994
<i>Cattleya labiata</i>		2.5		Hager, 1954
<i>Cattleya labiata</i> × <i>C. gaskelliana</i>	5.6			Burgeff, 1936
<i>Cattleya lawrenceana</i>		3.45		Shoushtari <i>et al.</i> , 1994
<i>Cattleya lobata</i>			76.86	Schlechter, 1915
<i>Cattleya mossiae</i>		3.12		Shoushtari <i>et al.</i> , 1994
<i>Cattleya percivalliana</i> × <i>C. aurea</i> ¶	4.3			Burgeff, 1936
<i>Cattleya reinekiana</i>		5.05		Shoushtari <i>et al.</i> , 1994
<i>Cattleya schroederiae</i>		6.76		"
<i>Cattleya trianae</i>			61.85	Schlechter, 1915; Shoushtari <i>et al.</i> , 1994
<i>Cattleya velutina</i> × <i>C. gigas</i>	4.6			Burgeff, 1936
Cattleya mean	4.94 ± 0.51	3.92 ± 1.48	79.24† ± 4.24	
<i>Cephalanthera austinae</i>			90.14	Tables 1,2
<i>Cephalanthera damasonium</i>		2.00	78.63	Rasmussen, 1995
<i>Cephalanthera damasonium</i>			60	Tables 1,2
<i>Cephalanthera grandiflora</i>	6.0		75	Burgeff, 1936
Cephalanthera mean	6.0	2.00	75.94 ± 12.43†	
<i>Corallorhiza innata</i>	7.2		83	"
<i>Cymbidium devonianum</i>	4.9			"
<i>Cymbidium eburneum</i>		3.77		Shoushtari <i>et al.</i> , 1994
<i>Cymbidium</i>			79.26	
<i>Cymbidium giganteum</i> ** × <i>C.</i> cv. Doris	3.0			Burgeff, 1936

<i>Cymbidium</i> hybrid		1.36		Cherevchenko & Kushnir, 1986
<i>Cymbidium insigne</i> × <i>C. lowianum</i>	4.6			Burgeff, 1936
<i>Cymbidium madidum</i>		4.46		Shoushtari <i>et al.</i> , 1994
<i>Cymbidium traceyanum</i> × <i>C. insigne</i>	5.0			Burgeff, 1936
<i>Cymbidium</i> mean	4.38 ± 0.93	3.20 ± 1.63	79.26†	
<i>Cypripedium</i> ††		2.0		Table 2
<i>Cypripedium acaule</i>		1.9	78	Tables 1,2
<i>Cypripedium calceolus</i> L.††	5.9		72.79	Mean from Tables 1,2
<i>Cypripedium californicum</i>			92	Table 1
<i>Cypripedium californicum</i> × <i>C. acaule</i>			90	"
<i>Cypripedium candidum</i>			89	"
<i>Cypripedium guttatum</i>	7.3			Burgeff, 1936
<i>Cypripedium montanum</i>			89	Table 1
<i>Cypripedium parviflorum</i>			93	"
<i>Cypripedium passerinum</i> ††			92	"
<i>Cypripedium pubescens</i> ††	8.1		94.5	Burgeff, 1936
<i>Cypripedium pubescens</i> × <i>C. acaule</i>			93	Table 1
<i>Cypripedium reginae</i>			87	"
<i>Cypripedium</i> mean	7.1 ± 1.11	2.0	88.21 ± 6.8†	
<i>Cyrtopodium punctatum</i>	5.1	3.4		Burgeff, 1936; Shoushtari <i>et al.</i> , 1994
<i>Didymoplexis pallens</i>	32.0	0.45		Burgeff, 1936
<i>Epipactis atrorubens</i>			85	"
<i>Epipactis gigantea</i>			88	Table 1
<i>Epipactis helleborine</i>			92	"
<i>Epipactis latifolia</i>	9.1		90	Burgeff, 1936; Tables 1,2
<i>Epipactis palustris</i>	7.5		92	"
<i>Epipactis rubiginosa</i>	6.8		90	"
<i>Epipactis</i> mean	7.8 ± 0.96		89.5 ± 2.67†	
<i>Eulophia</i>		2.73		Table 2
<i>Eulophia</i> × <i>Phaius flavus</i>	23.0			Burgeff, 1936
<i>Eulophia</i> mean	23.0	2.73		Table 2
<i>Goodyera</i> mean		2.00	71†	Tables 1,2
<i>Grammatophyllum speciosum</i>	7.8	2.48		Burgeff, 1936
<i>Gymnadenia conopsea</i> §§	4.8	8	98†	"
<i>Laelia</i>		3.05		Table 2
<i>Laelia anceps</i> × <i>L. cinnabarina</i>	4.3			Burgeff, 1936
<i>Laelia purpurata</i> × <i>Cattleya citrina</i>	4.5			"
<i>Laelia tenebrosa</i> × <i>Cattleya mendelii</i>	2.3			"
<i>Laelia</i> mean	3.7 ± 1.22	3.05		
<i>Limodorum abortivum</i>	3.7	5.7	98.68†	" ; Tables 1,2
<i>Liparis</i> mean	7.0		68†	
<i>Ludisia</i> mean	23	0.85		

Table 3 (cont.)

Species	Floatation in air (s)	Weight (μ g)	Air space (%)	Refs
<i>Odontoglossum</i> mean	6.3		48†	
<i>Orchis</i> mean	5.8		66.87†	
<i>Paphiopedilum</i> ††		3.00		Table 2
<i>Paphiopedilum</i> cv. <i>Albertianum</i> × <i>P.</i> cv. <i>Sallieri</i>	4.1			Burgeff, 1936
<i>Paphiopedilum argus</i>	6.1			"
<i>Paphiopedilum callosum</i> × <i>P. curtisii</i>	9.6			"
<i>Paphiopedilum charlesworthii</i>	3.5			"
<i>Paphiopedilum curtisii</i>	10.5		96	"; Tables 1,2
<i>Paphiopedilum insigne</i>			74	Table 1
<i>Paphiopedilum insigne</i> var. <i>sanderiae</i> × <i>P. concolor</i>	4.2			Burgeff, 1936
<i>Paphiopedilum lawrenceanum</i> × <i>P. glaucophyllum</i>	13			"
<i>Paphiopedilum spicerianum</i>	5.0			"
<i>Paphiopedilum</i> cv. <i>Superciliare</i> × <i>P. bellatulum</i>	11.0			"
<i>Paphiopedilum</i> cv. <i>Susan Tucker</i> × <i>P. parishii</i>			99	Arditti <i>et al.</i> , 1979
<i>Paphiopedilum tonsum</i> × <i>P. niveum</i>	12.0			Burgeff, 1936
<i>Paphiopedilum villosum</i> × <i>P. tonsum</i>	3.8			"
<i>Paphiopedilum</i> mean	7.53 ± 3.7	3.00	89.67 ± 13.65†	"
<i>Phaius flavus</i>	29.0			"
<i>Phaius maculatus</i>		3.53	76	Table 2
<i>Phaius</i> × <i>P. wallachii</i>	16.0			Burgeff, 1936
<i>Phaius</i> mean	22.5	3.53	76†	
<i>Phalaenopsis</i>			68.42	Table 1
<i>Phalaenopsis amabilis</i> × <i>P. rosea</i>			53.32	"
<i>Phalaenopsis aphrodite</i> × <i>P. sanderiana</i>	9.0			Burgeff, 1936
<i>Phalaenopsis mannii</i>		2.91		Shoushtari <i>et al.</i> , 1994
<i>Phalaenopsis sanderiana</i>	9.4			Burgeff, 1936
<i>Phalaenopsis</i> mean	9.2	2.91	60.87†	
<i>Platanthera bifolia</i>	6.8		82	Burgeff, 1936; Tables 1,2
<i>Platanthera chlorantha</i>	6.6		82	" "
<i>Platanthera dilatata</i> var. <i>leucostachys</i>			78	Healey <i>et al.</i> , 1980
<i>Platanthera hyperborea</i>			77	"
<i>Platanthera integrilabia</i>			57.55	Zettler & McInnis, 1994
<i>Platanthera saccata</i>			86	Healey <i>et al.</i> , 1980
<i>Platanthera</i> mean	6.7		77.09 ± 10.10†	
<i>Renanthera imshootiana</i>	11.6			Burgeff, 1936
<i>Schomburgkia undulata</i>	6.6	0.3		"
<i>Sobralia macrantha</i>	3.7	6.3		"
<i>Sobralia shoenbrunnensis</i> × <i>S. macrantha</i>	4.4			"

<i>Sobralia</i> , mean	4.05	6.3		
<i>Spathoglottis</i>	7.8		72	Burgeff, 1936; Table 2
<i>Stanhopea</i>		2.95		Table 2
<i>Stanhopea oculata</i>		3.00	89.31	von Marilaun, 1896; Fleischer, 1929, 1930; Burgeff, 1936
<i>Stanhopea oculata</i> × <i>S. quandricornis</i>	5.9			Burgeff, 1936
<i>Stanhopea</i> mean	5.9	2.95	89.31†	

Since information about weight, air space and floatation time for all taxa in this table is not available, data for related species or estimations for genera are included for comparison purposes. Mean and SD were calculated only when there were more than three values for any group. Given the small number of samples and the size of the Orchidaceae these numbers should be treated with caution. Names and their spelling used here are as in the original literature (except as indicated) because it is not possible to retroactively determine taxonomic identities.

Floatation in air (in seconds) was measured by H. Burgeff by dropping seeds in a glass tube (1.5 m long and 40 mm in diameter) and determining the time required for them to reach a white or black glass plate placed 50 mm below the top of the cylinder. First to reach the plate were seed clumps; they were followed by individual seeds; empty testae (i.e. chaff) were last. The error for descent times of 3–6 s was 0.1 s. For longer descent times (up to 30 s) the error was 5 s (Burgeff, 1936). A possible overall error in Burgeff's measurements may have been generated by the still air inside his cylinders. In nature there are always air swirls (even if sometimes very gentle ones) which could affect the floatation time of seeds.

*Burgeff may have meant *Calanthe sylvatica*.

†These values and a number of others were calculated from data in Tables 1 and/or 2 and/or our unpublished data. Because of that they are should be viewed as approximations. Calculations like these were made in cases where floatation times were available but not weights and/or percent air space.

‡This is probably *Laelia autumnalis*.

§Burgeff probably meant *C. harrisoniana*. This species is also known as *Cattleya loddigesii* var. *harrisoniana*.

||Another possible name for this orchid is *Laelia lobata*.

¶Yet another uncritical use of an orchid name by Burgeff; this is *Cattleya dowiana* var. *aurea*.

**Other names for this species are *Cymbidium lowianum*, *Eulophia speciosa* and *Iridorchis gigantea*.

††At one time *Cypripedium* included the genera that are presently known as *Cypripedium* and *Paphiopedilum*. When specific epithets and/or illustrations are not available in publications of that era it is often impossible to determine the identity of a '*Cypripedium*'.

‡‡Some taxonomists consider *Cypripedium calceolus*, *Cypripedium parviflorum* and *Cypripedium pubescens* as separate species. Others reduce the status of the last two to varieties of the first.

§§It is not unusual to see *Gymnadenia conopsea* or *Gymnadenia conopea* in the literature.

|||Burgeff does indicate that this is a hybrid.

Table 4. *Floataion of some orchid seeds in water and air*

Species (when available also seed weight (μg) and free air space (%))	Floataion time in air or water, or <i>Time for dry seeds to become wet and continue to float</i>						Refs
	Air (s)	Water			Duration of floataion f/s		
		Dry	Wetted	Difference			
<i>Acanthephippium sylhetense</i> (0.66 mg, 97.35 %)	13.0					Burgeff, 1936	
<i>Aceras anthropophora</i> (<i>Aceras</i> 66.67 %)						Ziegenspeck, 1935	
Immediate wetting					1		
Wetting after 1 h					2		
Wetting after 24 h					0		
Sinking after 24 h					2		
Wetting after 60 h					1		
Sinking after 20 h							
<i>Aerides quenquevulnerum</i> \times <i>Vanda tricolor</i>	8.0					Burgeff, 1936	
<i>Amerorchis rotundifolia</i>					f	Stoutamire, 1981	
<i>Anacamptys pyramialis</i>						Ziegenspeck, 1935	
Immediate wetting							
Wetting after 1 h							
Wetting after 24 h							
Sinking after 24 h					0		
Wetting after 60 h							
Sinking after 20 h					0		
<i>Angraecum eburneum</i>					s	Stoutamire, 1981	
<i>Angraecum eburneum</i> \times <i>A. sesquipedale</i>	9.0					Burgeff, 1936	
= <i>A. cv. Veitchii</i> (0.7 μg)							
<i>Angraecum sesquipedale</i>		0	0	0		"	
<i>Anguloa ruckeri</i> (0.39 μg)	13.0					"	
<i>Anguloa uniflora</i> \times <i>A. ruckeri</i>	10.0					"	
<i>Anguloa virginalis</i>					f & s	Stoutamire, 1981	
<i>Anguloa</i> mean	11.5 (0.39 μg)						
<i>Ansellia africana</i>					f	"	
<i>Aplectrum hyemale</i>					f	"	
<i>Aretusa bulbosa</i>					f	"	
<i>Bletilla hyacinthina</i>	3.5	2		2		Burgeff, 1936	
<i>Brassia verrucosa</i>	4.5					"	
<i>Brassia verrucosa</i> \times <i>Oncidium leucochilum</i>	4.5					"	
<i>Brassavola nodosa</i>					f & s	Stoutamire, 1981	
<i>Bulbophyllum macrobulbum</i>					f & s	"	
<i>Calanthe silvestris</i> (this is probably <i>C. sylvatica</i>) \times <i>C. cv. Darblayana</i> (0.5 μg)	12.0	1		1		Burgeff, 1936	
<i>Calanthe veratrifolia</i> \times <i>C. vestita</i>	13.0					"	
<i>Calanthe</i> mean	12.5 (0.5 μg, 78.74 %)						
<i>Calopogon pallidus</i>					f	Stoutamire, 1981	
<i>Calopogon tuberosus</i>					f	"	
<i>Calypso bulbosa</i>					f	"	
<i>Catasetum macrocarpum</i>			1		1	Burgeff, 1936	
<i>Cattleya</i>		1-4 to 7-8	1			Fleischer, 1929	
<i>Cattleya aurantiaca</i>					s	Stoutamire, 1981	
<i>Cattleya citrina</i>		9	1	8		Burgeff, 1936	
<i>Cattleya guttata</i> \times <i>C. autumnalis</i>	5.0					"	
<i>Cattleya guttata</i> var. <i>leopoldinae</i>	5.15					Shoushtari et al., 1994	

Table 4 (cont.)

Species (when available also seed weight (μg) and free air space (%))	Floation time in air or water, or <i>Time for dry seeds to become wet and continue to float</i>					Duration of floatation f/s	Refs
	Air (s)	Water			Difference		
		Dry	Wetted	Difference			
<i>Cattleya harrisoniae</i> \times <i>C. gaskelliana</i>	5.2						Burgeff, 1936
<i>Cattleya labiata</i> \times <i>C. gaskelliana</i>	5.6						"
<i>Cattleya percivalliana</i> \times <i>C. aurea</i> (this is probably <i>C. dowiana aurea</i>)	4.3						"
<i>Cattleya velutina</i> \times <i>C. gigas</i>	4.6						"
<i>Cattleya</i> mean	4.94 (3.94 μg, 79.24%)						
<i>Cephalanthera grandiflora</i>		28	5				Fleischer, 1929
<i>Cephalanthera grandiflora</i>	6.0	28	5	23			Burgeff, 1936
<i>Cephalanthera pallens</i>		23	5				Ziegenspeck, 1936
<i>Cephalanthera</i> mean	6.00 (2.00 μg, 76%)						
<i>Chysis bractescens</i>		1	0	1			Burgeff, 1936
<i>Cleistes divaricata</i>						f	Stoutamire, 1981
<i>Cochlioda neotzliana</i> \times <i>Odontoglossum</i> <i>crispum</i>	6.0						Burgeff, 1936
<i>Coeloglossum</i>		19	8				Ziegenspeck, 1936
<i>Coeloglossum viride</i>		19	8				Fleischer, 1929
<i>Coeloglossum viride</i>		27	8	19			Burgeff, 1936
<i>Coleglossum viride</i>		19	8				Ziegenspeck, 1936
<i>Coeloglossum viride</i>						f	Stoutamire, 1981
<i>Coelogyne cristata</i>						f & s	"
<i>Coelogyne huettneriana</i>			1			1	Burgeff, 1936
<i>Coelogyne macrocarpum</i>				1			"
<i>Corallorhiza</i>		60	6-8				Ziegenspeck, 1936
<i>Corallorhiza</i>		19	8				"
<i>Corallorhiza innata</i>		60	7				Fleischer, 1929
<i>Corallorhiza innata</i>	7.2	60	7	60			Burgeff, 1936
<i>Corallorhiza maculata</i>						f	Stoutamire, 1981
<i>Corallorhiza odontorhiza</i>						f	"
<i>Corallorhiza striata</i>						f	"
<i>Corallorhiza trifidida</i>						f	"
<i>Coryanthes macrantha</i>	11.0					30	Burgeff, 1936
<i>Cymbidium devonianum</i>	4.9						"
<i>Cymbidium giganteum</i> \times <i>C. cv. Doris</i>	3.0		3			3	"
<i>Cymbidium insigne</i> \times <i>C. lowianum</i>	4.6						"
<i>Cymbidium lancifolium</i>			3			1	"
<i>Cymbidium traceyanum</i> \times <i>C. insigne</i>	5.0						"
<i>Cymbidium</i> mean	4.38 (3.2 μg, 79.26%)						
<i>Cypripedium acaule</i>						f	Stoutamire, 1981
<i>Cypripedium arietinum</i>						f	"
<i>Cypripedium calceolus</i> (72.79%)		17	7				Fleischer, 1929
<i>Cypripedium calceolus</i>	5.9	25	7	17			Burgeff, 1936
<i>Cypripedium calceolus</i>		17	7				Ziegenspeck, 1936
<i>Cypripedium calceolus</i> var. <i>pubescens</i>						f	Stoutamire, 1981
<i>Cypripedium californicum</i>						f	"
<i>Cypripedium candidum</i>						f	"
<i>Cypripedium fasciculatum</i>						f	"
<i>Cypripedium guttatum</i>	7.3	60	6	60			Burgeff, 1936
<i>Cypripedium guttatum</i>						f	Stoutamire, 1981
<i>Cypripedium montanum</i>						f	"
<i>Cypripedium passerinum</i>						f	"
<i>Cypripedium pubescens</i> (94.5%)	8.1						Burgeff, 1936
<i>Cypripedium reginae</i>						f	Stoutamire, 1981
<i>Cypripedium</i> mean	7.1 \pm 1.11 (2 μg, 88.21 \pm 6.8)						
<i>Cyrtopodium punctatum</i> (3.4 μg)	5.1		1			1	Burgeff, 1936
<i>Cyrtopodium punctatum</i>						f	Stoutamire, 1981

Table 4 (cont.)

Species (when available also seed weight (μg) and free air space (%))	Flootation time in air or water, or <i>Time for dry seeds to become wet and continue to float</i>					Duration of floatation f/s	Refs
	Air (s)	Water			Difference		
		Dry	Wetted				
<i>Odontoglossum crispum</i> \times <i>O.</i> <i>triumphans</i>	7.2						Burgeff, 1936
<i>Odontoglossum grande</i>	5.2	1	0	1			"
<i>Odontoglossum grande</i>						s	Stoutamire, 1981
<i>Odontoglossum loochristiense</i> \times <i>O.</i> <i>inversum</i> \S	7.7						Burgeff, 1936
<i>Odontoglossum</i> mean	6.4 \pm 1.1						
<i>Odontoglossum pulchellum</i> \times <i>Miltonia</i> <i>warszewiczii</i>	5.8						"
<i>Odontoglossum</i> spp. and hybrids \parallel	6.3 \pm 1.0						
<i>Oncidium concolor</i> \times <i>O. marshallianum</i>	3.1						"
<i>Oncidium incurvum</i> \times <i>O.</i> <i>pulvinatum</i>	4.2						"
<i>Oncidium floridanum</i> (terrestrial race from Florida)						s	Stoutamire, 1981
<i>Oncidium forbesii</i> \times <i>O. marshallianum</i>	7.2						Burgeff, 1936
<i>Oncidium gartneri</i> (probably <i>gardneri</i>) \S \times <i>O. marshallianum</i>	4.8						"
<i>Oncidium marshallianum</i>	3.6						"
<i>Oncidium rogersii</i> \times <i>O. concolor</i>	5.9						"
<i>Oncidium splendidum</i> \times <i>O.</i> <i>cavendishianum</i>	4.3						"
<i>Oncidium</i> mean	4.7 \pm 1.4						
<i>Ophrys apifera</i>		3	3				Fleischer, 1929
<i>Ophrys apifera</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 h						4	
Wetting after 24 h						4	
Sinking after 24 h						0	
Wetting after 60 h						4	
Sinking after 20 h						3	
<i>Ophrys apifera</i>		6	3	3			Burgeff, 1936
<i>Ophrys apifera</i>		3	30				Ziegenspeck, 1936
<i>Ophrys aranifera</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 h							
Sinking after 24 h						0	
Wetting after 60 h							
Sinking after 20 h						0	
<i>Ophrys botteronii</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 h						4	
Wetting after 24 h						4	
Sinking after 24 h						0	
Wetting after 60 h						4	
Sinking after 20 h						3	
<i>Ophrys fuciflora</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 h							
Wetting after 24 h							
Sinking after 24 h						0	
Wetting after 60 h							
Sinking after 20 h						0	
<i>Ophrys lutea</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 h						3	

Table 4 (cont.)

Species (when available also seed weight (μg) and free air space (%))	Floatation time in air or water, or <i>Time for dry seeds to become wet and continue to float</i>					Duration of floatation f/s	Refs
	Water						
	Air (s)	Dry	Wetted	Difference			
<i>Spiranthes aestivalis</i>							Ziegenspeck, 1935
Immediate wetting							
Wetting after 1 hour						3	
Wetting after 24 h						3	
Sinking after 24 h						1	
Wetting after 60 h						3	
Sinking after 20 h						2	
<i>Spiranthes cernua</i>						f	Stoutamire, 1981
<i>Spiranthes cinnabarina</i>						f	"
<i>Spiranthes lacera</i>						f	"
<i>Spiranthes odorata</i>						f	"
<i>Spiranthes romanzoffiana</i>						f	"
<i>Stahopea oculata</i>			1			1	Burgeff, 1936
<i>Stanoppea oculata</i> \times <i>S. quadricornis</i>	5.9						"
<i>Stanhopea tigrina</i> (2.95 μg , 89.31 %)	3		1	2			"
<i>Sturmia</i>	41						Fleischer, 1929
<i>Sturmia</i>	41		6-8				Ziegenspeck, 1936
<i>Taeniophyllum</i> sp.						s	Stoutamire, 1981
<i>Thunia marshalliana</i>			2			2	Burgeff, 1936
<i>Tipularia discolor</i>						f	Stoutamire, 1981
<i>Traunsteinera globosa</i>							Ziegenspeck, 1935
Immediate wetting						1	
Wetting after 1 hour						3	
Wetting after 24 h						3	
Sinking after 24 h						0	
Wetting after 60 h						3	
Sinking after 20 h						2	
<i>Vanda coerulea</i> \times <i>V. suavis</i>	6.1						Burgeff, 1936
<i>Vanda suavis</i>	5.7						"
<i>Vanda tricolor</i> \times <i>V. burgeffii</i> §	5.0						"
<i>Vanda tricolor</i> \times <i>Vandopsis burgeffii</i> <i>lissocholooides</i>	6.3						"
<i>Vanda whiteana</i> (now <i>Vanda hindsii</i>)						s	Stoutamire, 1981
<i>Xylobium squalens</i>		7	0	7			Burgeff, 1936
<i>Zeuxine strateumatica</i>						f	Stoutamire, 1981
<i>Zeuxine reflexa</i>	39.0		3			3	Burgeff, 1936
<i>Zygopetalum mackayii</i>						f & s	Stoutamire, 1981

Except in a few instances, all names and their spelling as well as systematic affiliations are as given in the original literature. Much of the published information on the subject cannot be used here because it is presented in the form of vague qualitative statements. Only a few reports are quantitative, and even some of these are flawed because of faulty experimental procedures, fragmentary data and numbers that are not validated by statistics (e.g. Stoutamire, 1981).

The 'dry' column lists the number of days during which half of the seeds that were thoroughly shaken daily remained on the surface. Floatation time in days of seeds pre-wetted with alcohol is shown in the 'wetted' column; it was presented originally as a measure of the duration of the effects of air in the testa on seed buoyancy. The 'difference' column being the difference between 'dry' and 'wetted', was described as a measure of the duration of the effect that air which adheres to cell walls has on buoyancy (Burgeff, 1909, 1936). This measure assumes (probably inaccurately) that bathing with alcohol does not affect wetting of the testa and/or its coating. Data in the 'duration' column are from another experiment in which the seeds were shaken daily (Burgeff, 1936). The numbers in this case represent the duration of seed floatation on the surface in days. Numbers in **bold** represent the time it takes for dry seeds to become wetted and their floatation periods. These experiments were carried out in laboratory water or solutions that may have been different from natural effluates. *Means are in bold italics.*

Some of the data (Burgeff, 1909, 1936; Fleischer, 1929; Ziegenspeck, 1935, 1936) seem to be repetitions, but they are presented separately due to several differences, which suggest that they may have been copied incorrectly, obtained independently or derived from similar or repeat experiments. It is difficult to determine which if any of these possibilities is correct because later authors do not always cite earlier ones for reasons which are not clear.

Floatation in air (in seconds) was measured by dropping seeds in a glass tube (1.5 m long and 40 mm in diameter) and recording the time required for them to reach a glass plate placed 50 mm under the cylinder. First to fall on the plate

which the seeds are released (in orchids this can vary from a few centimetres in terrestrials to many metres above ground for epiphytic species); \bar{U} , mean wind speed; α , parameter associated with horizontal diffusion; β , parameter associated with atmospheric diffusion; \bar{A} , mean vertical diffusivity (which should be low in slow-dropping orchid seeds).

The parameters can be calculated from measurements of: number of seeds released per unit time; height of release (H); wind speed at H ; the settling velocity W_s ; and the dimensionless λ , which measures the relative spread about a mean for settling particles (Carey, 1998) that would be affected by air space in seeds (A. M. Ellison, pers. comm.). This equation produced a more satisfactory description of the distribution of *Himantoglossum hircinum* (Carey,

1998) despite the fact that air space in the seed (ca. 42%) and floatation time were not included in the equation. However, the calculation includes λ whose magnitude and effects can be expected to be the same as above (M. A. Ellison, pers. comm.). Altogether, orchid seeds can and do cover distances that may be as short as a few metres as suggested by Eqns 5 and 6, but also travel as far as thousands of kilometers (Table 5). The longer traveling will result from the increased variance and longer tail brought about by λ (Carey, 1998; Murren & Ellison, 1998). Given the many seeds produced by orchids, it is reasonable to assume that even if a small proportion will constitute the large variance and long tail, a sufficient number will travel far enough to colonize new areas: the available information is proof of that (Tables 4–6).

were seed clumps; these were followed by individual seeds; last to settle were empty testae. The error for descent times of 3–6 s was 0.1 s. For longer periods (up to 30 s) the error was 5 s (Burgeff, 1936). These measurements are not representative of natural conditions because the air inside the cylinder in Burgeff's laboratory was probably still. In nature the air moves constantly with varying velocities and directions even during a still day. These aerial eddies would tend to swirl the seeds and affect floatation time.

The tendency of orchid seeds to float or sink was investigated in several studies (Burgeff, 1909, 1936; Fleischer, 1929; Ziegenspeck, 1935, 1936; Stoutamire, 1981). In one of the earlier studies (Ziegenspeck, 1935) 10 ml of the 'purest distilled water' were poured into glass containers and then seeds were carefully dusted onto the surface. The water was then stirred carefully for 2 min. Wetting, floating and sinking were evaluated after 1, 24 and 60 h and listed on a scale of '–' (no wetting or sinking), $\frac{1}{4}$ –4 (degrees of wetting) and 5 (complete wetting). The evaluations seem to have been purely subjective, but the scale was given an appearance of great accuracy by the use of quarter fractions. However, these fractions and whole numbers are purely subjective. Further, water under natural conditions is not 'purest distilled' and may contain substances that could affect wetting and/or floatation.

In the more recent 'f/s' report (Stoutamire, 1981) the only information presented is whether the seeds float ('f') or sink ('s') after being shaken for one minute in distilled water. This is not representative because there is no distilled water in nature. A more appropriate liquid would have been an effluve, even one collected from cultivated plants sprinkled with water. Additional details about these determinations are not given. In a batch of seeds of a species or a hybrid some will float and others will not, especially if the suspension is not agitated or shaken. Shaking for one minute, even in water only, may increase the number of seeds that sink. More seeds will sink after longer and/or repeated shaking. The addition of surfactants and/or media components (or leachates in nature) may increase the wetting and/or reduce the surface tension of water, and therefore reduce floatation time with or without agitation. Seeds that do not sink immediately may do so with time (hours or days) even if they are not shaken. Also, chaff which can appear to the naked eye like embryo-containing seeds, may never sink. However, seed or chaff could sink if they become filled (to some extent at least) or completely saturated with water. These facts and the single 'treatment' (shaking for one minute) raise questions about the data produced by this study (Stoutamire, 1981), the validity of its findings and the value of the information it presents. The information is presented here simply because it provides at least some indications in a field for which good data are scant.

*Burgeff visited the Bogor Botanical Gardens in Indonesia c. 1930 and worked with plants of this orchid which grew inside a clump of bamboo near one of the gates. These plants were still growing and flowering there in 1969. They did not reappear in 1972 and failed to show up again until at least 1981.

†The genus *Galearis* has been equated with parts of *Orchis* and *Habenaria*. There is no *Habenaria spectabilis*. On the other hand there is an *Orchis spectabilis*, but its synonym is *Galeorchis spectabilis*. Also, *Galeorchis* is now a synonym of *Orchis*. A reasonable conclusion is that the original paper (Stoutamire, 1981) is in error and should have given the genus as *Galeorchis* or *Orchis*.

‡It is not uncommon to see these spellings. The correct spelling seems to be *G. conopsea*.

§These are examples of Burgeff's lack of care in the use of orchid names: *Odontoglossum* cv. *Loochritense* is not a species. It is a hybrid produced by the Belgian grower C. Vuylsteke who crossed *Odontoglossum crispum* (♀) with an unknown pollen source. It was first described in the British *Orchid Review* in 1898.

A species named *Odontoglossum inversum* could not be traced. An *Odontoglossum* cv. *Inversum* has not been registered. The closest similarity in names is *Odontoglossum* cv. *Inverness* which was registered in 1958, 22 years after Burgeff's book was published.

Oncidium rogersii (no authority is given in the original) is actually *Oncidium varicosum* var. *rogersii*.

'*Oncidium gartneri*' (no authority is given in the original) probably represents confusion due to the similarity between 'gardener' and 'Gardner' and the German equivalent *gärtner* and *Gartner*. It is *Oncidium gardneri*.

'*Paphiopedilum superciliare*' is actually *Paphiopedilum* cv. *Superciliare*, a hybrid between *Paphiopedilum barbatum* and *Paphiopedilum superbiens*.

'*Vanda burgeffii*' is actually *Vanda* cv. *Burgeffii*, a hybrid registered by the Munich Botanical Gardens in 1928. In the early days of orchid hybridization, hybrids were often given Latinized names by recognized orchid taxonomists like John Lindley and H. G. Reichenbach filius.

¶If Burgeff followed the current practice of listing the seed parent first it is not surprising that the seeds of the hybrid are similar to those of *Odontoglossum*.

Table 5. Distances travelled by some orchid seeds

Location or orchid	Distance covered	Refs
Agalega Island to Madagascar	600 km	Ridley, 1930
<i>Agrostophyllum majus</i>	81 m in Singapore	"
Aldabra to Madagascar	330 km	"
<i>Anacamptis pyramidalis</i>	'Some tens of kilometres' from the nearest population of this species	Willems, 1994
Andaman Islands to Tenasserim	480 km	Ridley, 1930
Australia to New Zealand	2000 km	Close <i>et al.</i> , 1978
Azores	1350 km	van Leeuwen, 1936
Azores to Madeira	825 km	Ridley, 1930
Azores to Portugal	1350 km	"
Bermuda to North Carolina, USA	870 km	"
Canary Islands to Cape Juby, Africa	75 km	"
Cape Verde Islands to Africa	750 km	"
Common dispersal distances	5–10 km	Lehaie, 1910 cited by Rasmussen, 1995
Christmas Island	200 km	van Leeuwen, 1936
<i>Cymbidium acutum</i> *	54 m in Singapore	Ridley, 1930
<i>Cymbidium finlaysonianum</i>	27 m in Singapore	"
<i>Dendrobium pandaneti</i>	1.5 km in Singapore	"
<i>Epipactis latifolia</i> †	12–15 km in the UK	Darwin, 1904
<i>Epipactis latifolia</i> †	12–14 km in England	Ridley, 1930
Galapagos	900 km	van Leeuwen, 1936
Hawaii	1000 km	"
Iceland to Greenland	375 km	Ridley, 1930
Kermadak	900 km	van Leeuwen, 1936
Krakatau	40–80 km	van Leeuwen, 1936; Went, 1957
Madeira to Morocco	675 km	Ridley, 1930
New Zealand from Australia	2000 km	Close <i>et al.</i> , 1978
No source or destination given	400 km	Garay, 1964
<i>Ophrys apifera</i>	60–75 km in Holland	Willems, 1994
Orchids, no names given	'Several hundreds of kilometres'	"
<i>Orchis militaris</i>	> 100 km	Willems, 1982 cited by Rasmussen, 1995
<i>Orchis simia</i>	c. 250 km	Crackles, 1975 cited by Willems, 1994
<i>Orchis simia</i>	< 25–200 km in Holland	Willems, 1994
Seychelles to Mauritius	1350 km	Ridley, 1930
Socotra to Cape Guardafui, Africa	750 km	"
Trinidad	900 km	van Leeuwen, 1936
Trinidad (south) to the South American mainland	900 km	Ridley, 1930
Unidentified orchid seed	1350 km	Dafni, 1981
Unidentified orchid seed	Found in the air 1800 m above sea level	"

Spelling of all geographic locations as well as taxonomic affiliations and names (except as below) are as they appear in the original sources. For reviews see Ridley (1930), Gandawijaja & Arditti (1983), Arditti (1992), and Rasmussen (1995). Reported distances of travel between smaller and larger islands and/or land masses are presented here because orchid seeds may have traveled and/or still do travel between them (Ridley, 1930). * This orchid is now classified as *Cymbidium dayanum*. † The current name is *Epipactis helleborine*.

<i>Cymbidium insigne</i> × <i>C. lowianum</i>	4.6										Burgeff, 1936
<i>Cymbidium traceyanum</i> × <i>C. insigne</i>	5.0										"
<i>Cymbidium</i> means	4.38	4000	89.26*	21 535 586	18 841 545	1.85×10^{-4}	2.13×10^{-4}	5384	4710	44.81	
<i>Cypripedium acaule</i>			78								J. Arditti & A. K. A. Ghani, unpublished
<i>Cypripedium acaule</i>		2000	85.51	33 912 000	28 999 602	5.90×10^{-5}	6.9×10^{-5}	16 956	14 500	23.39	"
<i>Cypripedium calceolus</i>			93								"
<i>Cypripedium calceolus</i>	5.9		90.98	16 249 274	14 784 645						Burgeff, 1936
<i>Cypripedium californicum</i>			92								J. Arditti & A. K. A. Ghani, unpublished
<i>Cypripedium californicum</i>			95.03	40 931 470	38 897 111						"
<i>Cypripedium californicum</i> × <i>C. acaule</i>			90								"
<i>Cypripedium candidum</i>			89								"
<i>Cypripedium candidum</i>			93.20	28 617 960	26 672 052						"
<i>Cypripedium guttatum</i>	7.3										Burgeff, 1936
<i>Cypripedium montanum</i>			87								J. Arditti & A. K. A. Ghani, unpublished
<i>Cypripedium montanum</i>			91	22 608 000	20 573 641						"
<i>Cypripedium passerinum</i>			94.58	34 265 250	32 407 792						"
<i>Cypripedium pubescens</i>	8.1		96								Burgeff, 1936
<i>Cypripedium pubescens</i> × <i>C. acaule</i>			93								J. Arditti & A. K. A. Ghani, unpublished
<i>Cypripedium reginae</i>			87								"
<i>Cypripedium</i> means	7.1	2000	90.35	29 430 659	27 055 897	6.8×10^{-5}	7.39×10^{-5}	147 159	1352	22.14	

<i>Eulophia</i> × <i>Phaius flavus</i>	23.0											Burgeff, 1936
<i>Eulophia</i> means	23.0	2730		13687643				2.0 × 10⁻⁴		5014		
<i>Galeola altissima</i>		17000		257900760				6.6 × 10 ⁻⁵		15171		Hamada & Nakamura, 1963
<i>Galeola lindleyana</i>		14000										Burgeff, 1936
<i>Galeola nudiflora</i>				1043333923								Barthlott & Ziegler, 1981
<i>Galeola septentrionalis</i>		24000										Nakamura, 1962, 1964
<i>Galeola</i> means		18333		650617342				2.8 × 10⁻⁵		35489		
<i>Goodyera procera</i>			88.84	8374908	7439875							Link, 1839–1842
<i>Goodyera pubescens</i>			68.24	2520227	1719765							Curtiss, 1893
<i>Geodorum densiflorum</i>			63.78	18780820	6801782							Singh & Thimmappaiah, 1982
<i>Geodorum</i> means	1.000		63.78	18780820	11978038							
<i>Geodorum pictum</i>	1.000											Hallé, 1977
<i>Goodyera repens</i>		2000	67.65	32149336	21747334							Curtiss, 1893; Downie, 1940; Arditti, 1992; Rasmussen, 1995
<i>Grammatophyllum speciosum</i>	7.8	2480										Burgeff, 1936
<i>Gymnadenia conopsea</i>	4.8	8000	93.92*							85.19		"
<i>Laelia</i>		3630										J. Arditti & A. K. A. Ghani, unpublished
<i>Laelia anceps</i> × <i>L. cinnabarina</i>	4.3											Burgeff, 1936
<i>Laelia purpurata</i> × <i>Cattleya citrina</i>	4.5											"
<i>Laelia tenebrosa</i> × <i>Cattleya mendelii</i>	2.3											"
<i>Laelia</i> means	3.7	3630										
<i>Limodorum abortivum</i>	3.7	5715	91.10*	40694400	37478784	1.4 × 10 ⁻¹	1.5 × 10 ⁻¹	7121	6559	62.73		Burgeff, 1936; Veyret, 1969; J. Arditti & A. K. A. Ghani, unpublished

Table 6 (cont.)

Species	Floatation in air (s) (F)	Weight (ng) (W)	Air space (%)	Volume (μm^3)		Ratios					Refs	
				Total (TV)	Free (FV)	W:TV	W:FV	TV/W	FV/W	W/%		
<i>Paphiopedilum Albertianum</i> × <i>P. Sallieri</i>	4.1											Burgeff, 1936
<i>Paphiopedilum argus</i>	6.1											"
<i>Paphiopedilum barbatum</i>				569125								Beer, 1863; Barthlott, 1976
<i>Paphiopedilum callosum</i> × <i>P. curtisii</i>	9.6											Burgeff, 1936
<i>Paphiopedilum charlesworthi</i>	3.5											"
<i>Paphiopedilum curtisii</i>	10.5		96.45	9385460	9052070							Schlechter, 1915; Burgeff, 1936; Hoene, 1949; J. Arditti & A. K. A. Ghani, unpublished
<i>Paphiopedilum insigne</i>		3000	27.78	8556067	2376090	3.5×10^{-4}	1.3×10^{-4}	2852	792	107.99		Zinger & Podubnaya- Arnoldi, 1966; Lucke, 1984a Burgeff, 1936
<i>Paphiopedilum insigne</i> <i>Sanderae</i> × <i>P. concolor</i>	4.2											"
<i>Paphiopedilum lawrenceanum</i> × <i>P. glaucophyllum</i>	13											"
<i>Paphiopedilum parishii</i>			99									"
<i>Paphiopedilum spicerianum</i>	5.0											"
<i>Paphiopedilum superciliare</i> × <i>P. bellatulum</i>	11.0											"
<i>Paphiopedilum tonsum</i> × <i>P. niveum</i>	12.0											"
<i>Paphiopedilum villosum</i> × <i>P. tonsum</i>	3.8											"
<i>Paphiopedilum</i> means	7.53	3000	97.5	6170217	5714080	3.5×10^{-4}	1.3×10^{-4}	2852	792	107.99		
<i>Phajus</i>			92.58	7065000	6540578							Davis, 1948
<i>Phajus flavus</i>	29.0											Burgeff, 1936
<i>Phajus maculatus</i>		3530										Shoushtari <i>et al.</i> , 1994
<i>Phajus Marthae</i> × <i>P. wallchii</i>	16.0											Burgeff, 1936
<i>Phajus</i> means	22.5	3530	92.58*	7065000	6540578	5.0×10^{-4}	5.4×10^{-4}	2001	1853	38.13		

<i>Phalaenopsis</i>			68.42	4108799	2811298						Linder, 1930; Bernard, 1937 Bernard, 1909
<i>Phalaenopsis</i> <i>amabilis</i> × <i>P. rosea</i>			15.91	1361975	216727						Burgeff, 1936
<i>Phalaenopsis aphrodite</i> × <i>P. sanderiana</i>	9.0										Shoushtari et al., 1994
<i>Phalaenopsis mannii</i>		2910									Burgeff, 1936
<i>Phalaenopsis sanderiana</i>	9.4										Burgeff, 1936
<i>Phalaenopsis</i> means	9.2	2910	42.17	1361975	216727	2.1×10^{-3}	1.3×10^{-2}	468	74.48	69.01	
<i>Platanthera bifolia</i>	6.8		82								Burgeff, 1936; J. Arditti & A. K. A. Ghani, unpublished
<i>Platanthera chlorantha</i>	6.6		82								Burgeff, 1936; J. Arditti & A. K. A. Ghani, unpublished
<i>Platanthera integrilabra</i>			57.55	20232758	1164335						Zettler & McInnis, 1994
<i>Platanthera</i> means	6.7		73.85	20232758	1164335						
<i>Renanthera imschootiana</i>	11.6										Burgeff, 1936
<i>Schomburgkia undulata</i>	6.6	300									"
<i>Sobralia macrantha</i>	3.7	6300									"
<i>Sobralia shoenbrunnensis</i> × <i>S. macrantha</i>	4.4										"
<i>Sobralia</i> means	5.05	6300									
<i>Stanhopea</i>		2910									Shoushtari et al., 1994
<i>Stanhopea oculata</i>		3000	89.31	12028398	10743062	2.5×10^{-4}	2.8×10^{-4}	4010	3581	33.59	von Marilaun, 1896; Fleischer, 1929, 1930; Burgeff, 1936
<i>Stanoppea oculata</i> × <i>S. quandricornis</i>	5.9										"
<i>Stanhopea</i> means	5.9	2955	89.31*	12028398	10743062	2.5×10^{-4}	2.8×10^{-4}	4070	3635	33.09	

Since information about weight, air space and floatation time for all orchids in this table is not available, figures for related species or estimations for genera are included for comparison purposes. The accuracy and reliability of these wide comparisons are clearly subject to errors. Total volume (TV) is the entire air space inside the testa. Free volume (FV) is the total volume minus the embryo volume.

Names used here are the ones given in the original literature.

Floatation in air (in seconds) was measured by dropping seeds in a glass tube (1.5 long and 40 mm in diameter) and measuring (with a stop watch) the time required for them to reach a white or black glass plate placed 50 mm under the cylinder. First to fall on the plate were seed clumps; individual seeds were next; the last to drop were empty testae. The error for drop times of 3–6 s was 0.1 s; for longer drop times, up to 30 s, the error was 5 s (Burgeff, 1936).

*These values and a number of others here were calculated from data for related species. Because of that some of them should be viewed as estimates. Calculations like these were made in cases where floatation times were available, but not sizes, weights and/or percent air space. The missing values generated by the calculations were used to construct several graphs (Figs 6,7) which depict relationships between floatation in air, weight, volume and percent air space ratios.

Box 2. Darwin's The Various Contrivances by Which Orchids are Fertilized by Insects

Darwin's *The Various Contrivances by Which Orchids are Fertilized by Insects* (Darwin, 1904) contains a valuable discussion of orchid seed number – despite the fact that he drew inaccurate conclusions. Note that Darwin did not italicize scientific names:

'The final end of the whole flower, with all its parts, is the production of seed; and these are produced by Orchids in vast profusion. Not that such profusion is anything to boast of; for the production of an almost infinite number of seeds or eggs, is undoubtedly a sign of lowness of organisation [inaccurate: orchids are now considered to be advanced plants]. That a plant, not being an annual, should escape extinction, chiefly by the production of a vast number of seeds or seedlings, shows a poverty of contrivance [inaccurate: orchids use almost all known contrivances to attract pollinators and disperse their seeds], or a want of some fitting protection against other dangers. I was curious to estimate the number of seeds produced by some few Orchids; so I took a ripe capsule of *Cephalanthera grandiflora*, and arranged the seeds on a long ruled line as equally as I could in a narrow hillock; and then counted the seeds in an accurately measured length of one-tenth of an inch. In this way the contents of the capsule were estimated at 6020 seeds, and very few of these were bad; the four capsules borne by the same plant would have therefore contained 24,080 seeds. Estimating in the same manner the smaller seeds of *Orchis maculata* [Fig. 1a], I found the number nearly the same, viz., 6200; and, as I have often seen above thirty capsules on the same plant, the total amount would be 186,300. As this Orchid is perennial, and cannot in most places be increasing in number, one seed alone of this large number yields a mature plant once in every few years.

To give an idea what the above figures really mean, I will briefly show the possible rate of increase of *O. maculata*: an acre of land would hold 174,240 plants, each having a space of six inches square, and this would be just sufficient for their growth; so that, making the fair allowance of 400 bad seeds in each capsule, an acre would be thickly clothed by the progeny of a single plant. At the same rate of increase, the grandchildren would cover a space slightly exceeding the island of Anglesea; and the great grand children of a single plant would nearly (in the ratio of 47 to 50) clothe with one uniform green carpet the entire surface of the land throughout the globe [see below]. But the number of seeds produced by one of our common British orchids is as nothing compared to that of some of the exotic kinds. Mr. Scott found that the capsule of an *Acropera* [Fig. 1b] contained 371250 seeds; and judging from the number of flowers, a single plant would sometimes yield about seventy-four millions of seeds. Fritz Müller [an early Darwin follower who wrote a book entitled *Für Darwin*; they corresponded at length, never met but held each other in high esteem – see Avadhani *et al.*, 1994] found 1756440 seeds in a single capsule of a *Maxillaria* [Fig. 1a–c]; and the same plant sometimes bore half-a-dozen such capsules. I may add that by counting the packets of pollen (one of which was broken up under the microscope) I estimated that the number of pollen-grains, each of which emits its tube, in a single anther of *Orchis mascula* [Table 1] was 122400. Amici estimated the number in *O. morio* [Tables 2, 3] at 120300 [in some cases this orchid can flower 23 months after sowing: Frosch, 1983]. As these two species apparently do not produce more seed than the allied *O. maculata* [Tables 2, 3], a capsule of which contained 6200 seeds, we see that there are about twenty pollen-grains for each ovule. According to this standard, the number of pollen-grains in the anther of a single flower of the *Maxillaria* [Fig. 1a–c] which yielded 1756440 seeds must be prodigious.'

Darwin's calculations for clothing the globe with *O. maculata* are impressive, particularly because they are for a plant which produces only 6200 seeds capsule⁻¹. The process would be much faster for an orchid like *Cychnoches ventricosum* var. *chlorochilon* (formerly *Cychnoches chlorochilon*), which produces 4000000 seeds per fruit (Table 2). Theoretically this species can produce $65\,536 \times 10^{24}$ individuals in four generations. The numbers for *Acropera* (*Gongora*) and *Maxillaria* would be 9×10^{31} and 144×10^{36} , respectively. *O. maculata* could produce as many as 81×10^{40} .

In the case of *Paphiopedilum*, the seeds of subgenus *Brachypetalum* are almost oval and 0.5–0.6 mm long (Karasawa & Saito, 1982). Examples of this subgenus are *Paphiopedilum concolor* (seeds oval, length 0.5 mm, air space 18%; Fig. 8), *Paphiopedilum bellatulum* (oval, 0.43 mm, 16%; Fig. 8) and their natural hybrid (according to Karasawa & Saito, 1982), *Paphiopedilum godefroyae* (oval, 0.35 mm and 23%; Fig. 8; percent air space calculated from measurements by Karasawa & Saito, 1982). The average air space of these seeds is 19%, and they probably have relatively short floatation periods. Species with such seeds can be expected to have a limited dispersal due to the constraints of the equations above and, indeed, this subgenus is found only in a contiguous land mass consisting of Burma, Thailand, southwest China, Yunan, Laos, Cambodia and Vietnam (Fig. 9; Karasawa & Saito, 1982; Cribb, 1987; Braem,

1988). Seeds of the subgenus *Sigmatopetalum* are longer. Examples are *Paphiopedilum callosum* (1.09 mm, 83%; Fig. 8), *Paphiopedilum ciliolare* (1.16 mm, 70%; Fig. 8) and *Paphiopedilum acmodontum* (0.79 mm, 69%; Fig. 8). These seeds have larger air spaces (an average of 74% or 3.9 times as much as *Brachypetalum*) and longer floatation times. Therefore their dispersal can be expected to be wider due to the increased variance and longer tail, and this is indeed the case. This subgenus is found in an area stretching from China through Java, Borneo, The Philippines and New Guinea to the Solomon Islands, even if the distribution of some species may be more limited (Fig. 9; Karasawa & Saito, 1982; Cribb, 1987; Braem, 1988).

Complicating factors in these considerations are the constant disagreement on taxonomy and nomenclature, and the short half-life of every 'new and

Box 3. Darwin on fruit and seed set in orchids

In Darwin's research on orchids, he produced important consideration of fruit and seed set. Note that Darwin did not italicize scientific names:

'The frequency with which throughout the world members of various Orchideous tribes fail to have their flowers fertilised, though these are excellently constructed for cross-fertilisation, is a remarkable fact.

Fritz Müller informs me that this holds good in the luxuriant forests of South Brazil with most of the Epidendreae, and with the genus *Vanilla*. For instance, he visited a site where *Vanilla* creeps over almost every tree, and although the plants had been covered with flowers, yet only two seed-capsules were produced. So again with an *Epidendrum*, 233 flowers had fallen off unimpregnated and only one capsule had been formed; of the still remaining 136 flowers, only four had their pollinia removed. In New South Wales Mr. Fitzgerald does not believe that more than one flower out of a thousand of *Dendrobium speciosum* sets a capsule; and some other species there are very sterile. In New Zealand over 200 flowers of *Coryanthes triloba* yielded only five capsules [see below] and at the Cape of Good Hope only the same number were produced by 78 flowers of *Disa grandiflora*. Nearly the same result has been observed with some of the species of *Ophrys* in Europe. The sterility in these cases is very difficult to explain. It manifestly depends on the flowers being constructed with such elaborate care for cross-fertilisation, that they cannot yield seeds without the aid of insects. From the evidence which I have given elsewhere we may conclude that it would be far more profitable to most plants to yield a few cross-fertilised seeds, at the expense of many flowers dropping off unimpregnated, rather than produce many self-fertilised seeds. Profuse expenditure is nothing unusual under nature, as we see with the pollen of wind-fertilised plants, and in the multitude of seeds and seedlings produced by most plants in comparison with the few that reach maturity. In other cases the paucity of the flowers that are impregnated may be due to the proper insects having become rare under the incessant changes to which the world is subject; or to other plants...'

Note that the genus *Coryanthes* and its pollinators are indigenous to Central and South America. There is no reason why it should set seed in New Zealand (unless hand-pollinated). In discussing *Coryanthes triloba* Darwin probably meant *Corysanthes trilobus*, now reclassified as *Corybas trilobus*. *Corybas* (*Corysanthes*) is native to New Zealand. *Corysanthes* and *Coryanthes* do not even resemble each other.

improved' classification system (the *Paphiopedilum* classification used here is that of two Japanese cytologists, Karasawa & Saito, 1982). Another classification could produce different or no correlations. As with examples in all areas of orchid biology it is necessary to keep in mind that the Orchidaceae is a large, complex and varied family and all models must be treated with caution. Very often it is necessary to use limited or even single

samples because there are no others. Even competent studies (Carey, 1998; Murren & Ellison, 1998) are limited by technical and biological constraints to only a single species each (fusiform, $640 \pm 40.6 \times 56 \pm 4.8 \mu\text{m}$, $1.6 \mu\text{g}$ for *Brassavola nodosa* and fusiform but stubby, $130 \times 30 \mu\text{m}$ and $5 \times 10^{-9} \text{kg}$ for *Himantoglossum hircinum*). Would larger or smaller and/or heavier or lighter and/or differently shaped seeds give the same result?

(c) *Birds*. It is a mistake to assume that all travel by orchid seeds is through floatation in the air. For example, it was generally assumed that orchid seeds reached Krakatau on wind currents (van Leewen, 1936; Went, 1957; Garay, 1964; Gandawijaja & Arditti, 1983) following the volcanic eruption and destruction of the island in 1883 (Simkin & Fiske, 1983). However, Went (Went, 1957, 1990; F. W. Went, pers. comm.) suggested that orchid seeds could have reached the island on the legs or feathers of birds (exoornithochory). If transported on the legs of birds in mud or even on feathers the seeds probably arrived together with spores of fungi which could establish a mycorrhizal association and make germination possible (Went, 1957; F. W. Went, pers. comm.; Mitra, 1971; see Gandawijaja & Arditti, 1983).

Transport by birds, which is relatively quick, is also favoured because of the rapid loss of viability by seed stored under conditions that are generally unfavourable (Lucke, 1985) and/or permit rapid desiccation (Arditti, 1967, 1979, 1992; Arditti & Ernst, 1984). Conditions during long air-floatation periods (i.e. flights) may also lead to desiccation (Garay, 1964). Transport on muddy feet of birds or their feathers could reduce desiccation and make possible wider dispersal (Garay, 1964; Gandawijaja & Arditti, 1983).

According to one view, transport inside birds (endoornithochory) is not a means of orchid seed dispersal because of their inability to 'withstand the digestive fluids of birds' (Garay, 1964). On the other hand there are indications that seeds of *Vanilla planifolia* and *Galeola septentrionalis* (probably similar to those of *Galeola galeata* and *Galeola altissima* Fig. 1b) may be endoornithochorous (Nakamura & Hamada, 1978). The seeds of the latter may also be or endozoochorous (Hamada & Nakamura, 1978). There is also a report that orchid seeds are scattered widely with excrement (Beer, 1863; Nakamura & Hamada, 1978). Treatments with a variety of solvents and surface sterilants suggest that orchid seeds may be able to withstand digestive tracts at least for a while (see Arditti, 1967, 1979, 1992; Arditti & Ernst, 1984). It is possible that ingestion by birds may even enhance germination of *Vanilla planifolia* seeds because of chemical changes brought about by 'juices' in the intestinal canal (Bouriquet, 1943; Stoll, 1954; Nakamura & Hamada, 1978). Chemical attack by digestive fluids could facilitate

germination by rendering the testa more permeable to water. Thus, endoornithocory and endozoochory cannot be fully excluded without experimental evidence. Some pertinent albeit indirect evidence should be relatively easy to obtain because the nature of digestive tracts and fluids in birds and other animals are known and could be simulated in a laboratory where orchid seeds can be subjected to them.

2. Water

(a) *Physical considerations.* Orchid seeds can float on water for prolonged periods (Table 4; Burgeff, 1936; Ziegenspeck, 1935, 1936; Rauh *et al.*, 1975; Stoutamire, 1981; Rasmussen, 1995) for the following reasons:

- They are filled with air (Table 1; Ziegenspeck, 1935, 1936; Carlson, 1940; Arditti, 1967, 1979, 1992; Arditti *et al.*, 1979, 1980; Healey *et al.*, 1980; Barthlott & Ziegler, 1981; Tohda, 1983; Arditti & Ernst, 1984).
- Their testae are hard to wet (Burgeff, 1936; Ziegenspeck, 1936; Arditti *et al.*, 1982; Rasmussen, 1995).
- The structure of the testa enhances floatation as in the case of *Disa uniflora* and several related species (Kurzweil, 1994).
- Buoyancy is enhanced by air bubbles trapped in the sculpturing of the testa (Ziegenspeck, 1936; Rasmussen, 1995).

Agitation (shaking or stirring) was employed in most experiments designed to study the floatation of orchid seeds in water. This seems to be a reasonably good approximation of natural condition because seeds may float in and be carried by moving, eddying and bubbling tree effluates and/or streams or rivulets of various sizes and velocities, which provide agitation. However, treating seeds with solvents, surfactants and/or other chemicals prior to floatation experiments could not possibly produce representative results because these treatments change the nature of the testa and/or any coating that may cover it as well as the surface tension of water. For example, surfactants accelerate the sinking of seeds in sodium hypochlorite solutions (Arditti *et al.*, 1982). Hypochlorite (calcium and sodium) solutions in themselves also alter the outer chemical nature of the testa (Rasmussen, 1995). These changes undoubtedly affect wetting of the seeds and, as a consequence, also their floatation. Even distilled water (Stoutamire, 1981) is not a good approximation because under natural conditions water that may carry orchid seeds is actually a solution containing minerals and organic leachates, which could affect the testa.

Orchid seeds are difficult to wet because the outer walls of their testa cells are hard, lignified and

covered with a cuticle (Ziegenspeck, 1936). The inner walls have no cuticle and are thinner. As the seeds ripen testa cells lose moisture and their walls curve inwards (Ziegenspeck, 1936). Both the cells and testas are filled with air. A mechanism that brings about the wetting of these hard to wet seeds was proposed more than half a century ago (Ziegenspeck, 1936). When seeds that fall into water or drop onto a moist substrate are chilled by cool water or reduced atmospheric temperatures the air inside the testa contracts. This creates suction that draws water into the seed through the micropylar opening (Fig. 3, 4; Ziegenspeck, 1936). Once inside the seeds, water enters testa cells through their thin inner walls (Ziegenspeck, 1936). Such a mechanism probably works well wherever even a small temperature differential follows the release of orchid seeds.

In addition to entering testa cells from the inside, water within the seed also hydrates the embryos. The hydration causes the embryos to enlarge and emerge from the testa. Limited metabolic activity is also initiated in the hydrated seeds. Embryos may even turn green but do not develop into seedlings until they are colonized by an appropriate mycorrhizal fungus. Under laboratory conditions seeds placed on a medium that contains only minerals use their resources very slowly. Even the limited reserves inside the seeds are sufficient for survival periods of a year or more (Arditti, 1967, 1979, 1993, 1992). In nature, such long survival (almost suspended animation) periods increase the chances of fungal penetration. Thus the reserves in orchid seeds function not in sustaining germination, but in supporting the seeds until seedling development becomes possible. Clearly the evolution of orchid seeds is an exquisite contrivance that ensures dispersal and survival.

(b) *Dispersal.* Orchid seeds may not have been carried to Krakatau by ocean currents because they were reported to 'lose their viability after extended immersion in salt water' (Garay, 1964). At present there is no information about the tolerance (or lack of it) of orchid seeds to sea water and/or saline conditions. It is also not known whether seeds will germinate after immersion in sea water and subsequent deposition onto terrestrial substrates (saline or not) such as rocks of phorophytes. This could be tested by immersing seeds in sea water for various periods and then attempting to germinate them. Orchid plants sometimes grow on rocks or trees near or over oceans where they are subjected to salt water mist or spray (Arditti, 1992). Seeds obviously germinate under these conditions, but it is not clear whether such germination is limited only to a few species that have adapted to salinity.

There is no doubt that orchid seeds fall into oceans (on Malaita, Solomon Islands several orchids, some in bloom, others in fruit grew on tree branches hanging from trees on rocky beaches; J. Arditti, unpublished). If orchid seeds could be carried by

ocean currents they would be washed onto sandy or rocky beaches, not the interior of land masses, except if blown inland by wind after being deposited at the water's edge; carried inward in ocean mist; jettisoned onto seaside rocks and/or trees in the spray that results from crashing waves; and/or moved to the interior on the feet of animals that come to beaches. These possibilities have not been studied.

Fresh water does not seem to affect orchid seed deleteriously. Seeds of *Disa cardinalis*, *Disa uniflora* and *Disa tripetaloides* 'fall into streams and float down the water surface (this can be directly observed; due to their large size the seeds can be seen with the naked eye!)...and most of the seedlings occur on the banks of streams' (Kurzweil, 1994). European orchids are carried by rain water to areas where the soils are appropriate for germination (Fleischer, 1929; Burgeff, 1936; Ziegenspeck, 1936). In the tropics orchid seeds germinate on tree barks (Frey & Dodson, 1972).

VI. CONCLUSIONS

Another quotation from Darwin points to one function of the small, light, air-filled and buoyant orchid seeds (scientific names not italicized):

'The minute seeds within their light coats are well fitted for wide dissemination; and I have several times observed seedlings springing up in my orchard and in a newly-planted wood, which must have come from a considerable distance. This was especially the case with *Epipactis latifolia*; and an instance has been recorded by a good observer of seedlings of this plant appearing at the distance of between eight and ten miles from any place where it grew...'

He also noted that:

'species...are sparingly distributed; yet, if their seeds or seedlings were not largely destroyed, any one of them would immediately cover the whole land...The number of the individuals which come to maturity does not seem to be at all closely determined by the number of seeds which each species produces; and this holds good when closely related forms are compared.'

Among post-Darwinian deliberations regarding the nature of orchid seeds and their role in the evolution, dispersal, life cycle and physiology of orchids none are as perceptive and lucid as those by David Benzing (Benzing, 1981). His discussions are based on five generally accepted premises regarding orchids '(1) Orchidaceae is probably the largest of all angiosperm families [but similar claims are being made for the Asteraceae]; (2) its seeds are among the smallest of any taxon; (3) the resulting seedlings are mycotrophic; (4) many of its species are rare or widely dispersed; and (5) they often rely on very specialized pollination relationships...' and on one question: '...what about the tiny seeds and unusual mode of seedling nutrition? Individual seeds...[may weigh]...0.01–0.1 mg for many orchids...'

Benzing enumerates 'three distinct requirements' which necessitate 'close adherence to an optimal profile: (1) the heterotrophic demand of a seedling before it achieves autotrophy; (2) the need for dispersal to propitious sites; and (3) the necessity for sufficient fecundity to maintain a parent population.' He also points out that the characteristics of orchids seeds vary among taxa due to tradeoffs that are brought about by the need to survive under numerous 'combinations of constraints in native habitats.' One of these habitats, 'the patchy and infertile nature of the epiphytic biotope' is 'the rationale for the high fecundity and vagility required of plants living in the crowns of trees'.

Studies by Benzing and his associates (Benzing, 1981, 1987) showed that for epiphytes small seeds are advantageous because they increase the 'mineral economy and [counter] the high rates of juvenile mortality'. Terrestrial orchids also have to contend with inhospitable environments like 'infertile acid bogs and porous soils,' and 'physical constraints for some time'. On the basis of his considerations Benzing suggested 'that the seeds of orchids have become unusually small in response to strong reselecting forces imposed by unpredictably disturbed, patchy and stressed habitats. The miniaturization required to achieve a 'dust' type seed – the basis of the impressive fecundity mounted by these organisms – seems to have been made possible by major shifts in juvenile nutrition that, in effect, obviated the need for maternally supplied food at germination and for varying periods of time afterwards.'

The dependence of orchid seeds on mycorrhizal fungi for germination supports Benzing's views because it explains how young orchid seedlings survive in the field with very limited food reserves and an impaired ability to use what little they do have (Arditti, 1967, 1979, 1992; Arditti & Ernst, 1984; Arditti *et al.*, 1990). During the early stages of germination orchid seedlings obtain nutrients from their fungi. In fact the orchids parasitize the fungi and this relieves the orchid embryo of its reliance on endogenous sources of nutrients. To put it differently, orchid seeds are small because they can get away with not having an internal endosperm. They obtain nutrients from an exogenous 'endosperm' (i.e. the fungal symbiont). Thus, Benzing concludes, 'a maternal parent, freed from the usual task of provisioning its young with substantial nutrient stores, is amenable to selective forces that encourage the production of unusually large numbers of small seeds'.

These 'unusually large numbers of small seeds' are neither wasteful burdens on the Orchidaceae nor 'lowness of organisation' or 'a poverty of contrivance'. They are two reasons for the success of the family.

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