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HARDY ORCHID SOCIETY**



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Cover Photographs

Front Cover: Peter Cowin's photograph of *Disa ferruginea*; see page 134 for Peter's article on South Africa's Table Mountain.

Back Cover: Alan Smith's photograph of an unusual Bee Orchid; see page 140 for Alan's article on *Ophrys apifera* variants.

The Hardy Orchid Society

Our aim is to promote interest in the study of Native European Orchids and those from similar temperate climates throughout the world. We cover such varied aspects as field study, cultivation and propagation, photography, taxonomy and systematics, and practical conservation. We welcome articles relating to any of these subjects, which will be considered for publication by the editorial committee. Please send your submissions to the Editor, and please structure your text according to the “Advice to Authors” (see Members’ Handbook, website www.hardyorchidsociety.org.uk, or contact the Editor). Views expressed in journal articles are those of their author(s) and may not reflect those of HOS.

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**Editorial Note
Mike Gasson**

In our 25th Anniversary year it is a pleasure to able to include a new major article from our President Professor Richard Bateman in this *JHOS*. Richard already contributed an impressive and entertaining lecture at the Kidlington Spring Meeting, so I am really grateful that he has also found the time and energy to give us such an interesting and authoritative overview of orchid systematics here. The Society is very fortunate to have a leading academic scientist amongst its members and one who has given so much support to HOS over very many years.

With this major article, space for additional contributions was a little limited this time but I have tried to include a little colour in the form of Peter Cowin’s account of Disas on South Africa’s Table Mountain. Also a rather more light hearted piece from Alan Smith, describing some weird and wonderful Bee Orchid variants.

Sorry to those members waiting for their articles to appear. I hope to manage a little catching up over the next couple of issues as we are fortunate in having a fair number of good articles already submitted. Even so please keep up the good work and do keep sending in contributions for *JHOS*!

Chairman's Note

Colin Scrutton

First of all, you may remember that the last talk for the November meeting was still to be arranged when the booking form went out. Our Speaker Secretary, Celia Wright, has now completed the programme, which is included here on the following page. I look forward to a good turnout at the meeting on 18th November at Kidlington.

I mentioned in my last note that we would miss most of the domestic orchid season with a longish trip to Australia. We also missed most of the long, hot summer as well! The latter rather overwhelmed the later flowering orchids so that by the time we returned all we could do was to await the appearance of the Autumn Lady's-tresses, assuming that the prolonged heat and lack of rain had not done for them as well.

Our Australian trip was most successful and we photographed nearly all of our targets. Since returning we have been helping friends of ours, fellow members of HOS, with useful locality details in WA. In one email, they wrote "What should we be keeping an eye out for so that we do not get lethally bitten or stung?" As they noted, health and safety whilst searching for orchids is not something that is much discussed. Perhaps we are all reasonably aware of what to watch out for in the UK and the rest of Europe, from biters and stingers to animals farmed and wild. But Australia does have rather a lot of potentially death-dealing inhabitants. During geological trips there and later with Angela searching for orchids, I have taken my guidance from our Australian friends and colleagues, who are generally relaxed about bush-bashing for the most part. Don't creep silently through the bush but make some noise (Angela now uses her walking poles to good effect). Snakes will almost invariably slither away. The Tiger Snake is reputed to be the most aggressive but the only time we have seen one, coiled up beneath shrubs near a path, it watched us pass without stirring (it was alive!). Snake anti-venom is widely available across Australia and deaths from snake bites are very rare. Take care if you pick stones up as there could be something dangerous underneath. I once had the experience in a quarry when I picked up a lump of limestone with a fossil in it to find a Redback Spider lurking on the underside. Be careful in bush dunnies as Redbacks can lurk beneath the seat! The Sydney Funnel-web Spider is much more dangerous but restricted to the Sydney area of New South Wales and generally more active at night. Angela, whose flesh is considered particularly succulent by various biting insects, tucks the bottom of her trousers into her socks, which seems to minimise that problem. The possible risks of swimming in the sea are well reported but if you visit the Northern Territories, don't go swimming in a billabong unless you know it is safe as salt-water crocodiles get stranded in them when the "wet" rainy season changes to the "dry". We have never had any problems in all our trips taking reasonable care, nor have any of our Australian friends and colleagues. However, there is one thing to watch out for

wherever you are and particularly in Australia, and that is ticks. I have occasionally picked up a tick in the UK or Europe but in the Australian bush it is a common event. You need to keep square ended tweezers with you and some knowledge as to how to extract a tick safely. Australians claim that their ticks do not carry Lyme Disease, but European ticks can. The wife of a colleague spent a year or so in a wheelchair after catching Lyme Disease from a tick bite. Fortunately she made a complete recovery in the end. One final problem in wetter areas is leeches. You may not notice them until the end of the day when changing or taking a shower, which happened to me on the Tasmanian Cradle Mountain walk. An application of salt will cause them to drop off. The spot might itch for a few days if you have sensitive skin but otherwise there should be no ill effects! So, we can recommend a visit to Australia, which has superb orchid flora both east and west with little species overlap between the two areas. Just take reasonable care when exploring the bush!

Programme for HOS Southern Autumn meeting at Kidlington
 Sunday 18th November 2018

9:00		Set up trade and members' stands. Staging of Photographic Competition.
9:30		Doors open, sales begin. Tea and coffee available. Photographic entries to be in by 10.30 am when judging begins.
10:30	Colin Scrutton (Chair)	Introduction.
10:40	Celia Wright	Finding & Growing <i>Cypripediums</i> in SW China.
11:40		<i>Short Break</i>
11:50	Andrew Bannister	An update on the <i>Cypripedium calceolus</i> reintroduction programme and its cultivation.
12:50		Winning film from Video Competition held at Leeds meeting.
13:00		<i>Lunch</i> and opportunity to view the Photographic Competition.
14:00	Jon Evans	Photographic competition judging and results.
14:45	Rosie Webb	Special orchid finds in Hampshire.
15:45		<i>Tea Break</i>
16:00	Iain Wright	Some orchids of Sikkim.
16.30		Meeting ends. Hall must be vacated by 5pm.

Systematics Research into Hardy Orchids: Recent Successes and Future Prospects

Richard Bateman

It is my great pleasure to record, in this summary of a HOS anniversary lecture given in April 2018, the 25 years of progress achieved since the HOS came into existence in the sciences of systematic biology and evolution. I have chosen to do so by first reviewing where orchid research stood a quarter century ago in 1993, then taking an overview of recent research on Europe's most troublesome orchid genus, and finally speculating on whether technological advances in the immediate future might offer to all enthusiasts enhanced opportunities to contribute to orchid studies.

When preparing this article I have elected to remain on home turf, focusing on the European orchid flora and emphasising progress in DNA-based studies. Although I realise that I am risking accusations of bias, I genuinely believe that the impact of DNA techniques has been considerably greater than that of any other investigative approach. Admittedly, in preparing this review I encountered a few surprises. Most notably, several technological advances proved to have been made earlier than I had realised; it seems that the typical dissemination pattern of novel analytical techniques through the scientific community begins with research oriented toward improving welfare for humans, then farm animals, and then crop plants. Consequently, the cutting edge of technology typically reaches orchid studies only comparatively late in time, inevitably placing them lower in the pecking order when competing for substantial research grants.

Orchid studies around 1993

In terms of the appearance of noteworthy orchid books, 1993 fell in the middle of a comparatively fallow period. Summerhayes' *Wild orchids of Britain* (twice lightly updated since its release in 1951) still held sway in the UK, whereas several books published during the 1980s competed to summarise the European orchid flora. The most important orchid book published during 1993 was Dressler's *Phylogeny and classification of the orchid family*, which used as its framework some crude but well-informed morphology-based evolutionary trees. Also published during 1993, and presaging the excellent production quality of the first (1994) edition of Delforge's *Guide des orchidées d'Europe*, was *Wild orchids of Scotland* – a book produced to coincide with the 14th World Orchid Congress convened in Glasgow.

It is by examining the multi-author *Proceedings* of the conference that we can best assess the rather parlous condition of orchid research in 1993. Admittedly, the conference volume was incomplete – for example it scandalously failed to capitalise on the computer-based approach to morphometric analyses pioneered a decade earlier by young turks Bateman & Denholm! Nonetheless, the *Proceedings*

included articles on topics as disparate as micromorphology (i.e. detailed anatomy) and development of seed embryos into protocorms, while elsewhere was published the fine-mesh netting technique needed to recover orchid seeds after they have germinated *al fresco*. Detailed chromosomal studies summarised in the volume unwittingly pre-empted the 1997 DNA-based re-circumscription of species into three genera formally encompassed by the genus *Orchis*. In ecology, fixed-grid demographic studies of orchid populations that had begun in the 1960s were finally yielding statistically robust data, though biochemical analysis of orchid fragrances remained in its infancy.

Perhaps most importantly, the first comparative study of orchids based on DNA data was published in the *WOC Proceedings*. At this point, I think it will help to clarify the remaining discussion if I remind readers once again that any plant cell contains not just one but three genomes: nuclear, plastid and mitochondrial (Fig. 1). Most genes are held in the nuclear genome, which consists of chromosomes inherited equally from the plant's 'mother' (ovule parent) and 'father' (pollen parent). However, numerous organelles also occur within each cell. Inherited exclusively from the mother, the organelles each contain their own smaller genomes: the plastids are responsible for photosynthesis, and the mitochondria (which play no role in the present story) are responsible for respiration.

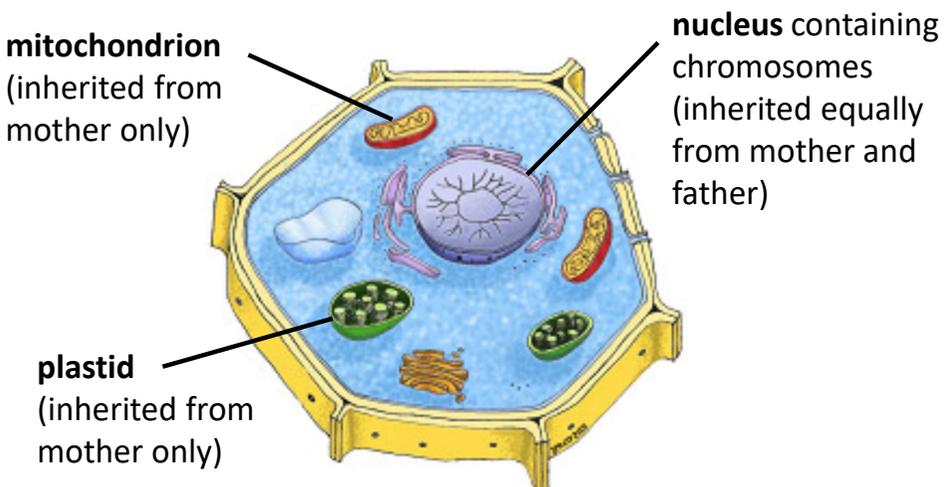


Fig. 1: Reminder that each plant cell contains not just one but three distinct genomes: the nuclear (chromosomal) genome inherited equally from both parents, and the plastid and mitochondrial genomes inherited only from the 'mother' (ovule parent).

The ground-breaking study summarised in the WOC *Proceedings* used a single chloroplast gene and spanned the entire orchid family, albeit favouring tropical genera over their temperate cousins. Remarkably, the year 1993 also yielded the first study of a nuclear (i.e. chromosomal) gene that actually influences orchid morphology. However, only one tropical orchid species was analysed, simply to allow comparison with petunias, yeasts and humans! These molecular studies of the early–mid 1990s were benefiting from a recent technological advance that replaced data-deficient radioactive labelling of DNA bases (i.e. the four DNA ‘letters’: A, G, C and T) with labelling based on coloured stains. This semi-automated ‘Sanger’ sequencing made gathering DNA data both more streamlined and less dangerous, though it still targeted very small regions of the genome already proven to be informative regarding evolutionary relationships – termed the ‘candidate gene’ approach. These early molecular papers laid the groundwork for more ambitious and far better sampled comparative studies of orchid sequences in the late 1990s and early 2000s – studies that provided a valuable evolutionary-phylogenetic framework for the entire European orchid flora and led to radical reallocation of species among several European orchid genera. Thus was the scene duly set for further advances in the 21st Century.

Does *Ophrys* consist of microspecies, mesospecies or macrospecies?

The best way for me to summarise current European orchid studies with acceptable brevity is to explore a particularly challenging genus in greater detail. I have therefore elected to review progress in the study of the most biologically intriguing and taxonomically troublesome of all European orchid genera, *Ophrys* (one of my favourite topics, yet one that, I was surprised to discover, I have never previously addressed directly in the pages of this particular journal). A more detailed account, written with somewhat different emphases, can be found in Bateman (2018).

In order to discuss cogently the many problems surrounding the circumscription and subsequent identification of *Ophrys* taxa, I will first introduce a novel terminology capable of distinguishing the nine species recognised in the most recent genus-wide DNA sequencing study (Bateman *et al.* 2018) from the 353 ‘species’ that together occupy 224 pages of the most recent edition of Delforge’s (2016) benchmark European orchid monograph. Specifically, I will refer to the nine species recognised by Bateman

Figs. 2–10: Floral morphology of selected *Ophrys*. (2–4) Three examples of *Ophrys* macrospecies: *O. apifera* (2), *O. umblicata* (3), *O. fuciflora* (4). (5–7) Three examples of *Ophrys* mesospecies within the *O. sphegodes* macrospecies: *O. reinholdii* (5), *O. bertolonii* (6), *O. ferrum-equinum* (*mammosa* mesospecies) (7). (8–10) Three examples of microspecies within the *O. incubacea* mesospecies: *O. incubacea* (8), *O. passionis* (*garganica*), (9), *O. aveyronensis* (10). Horizontal dimension of all images = 22 mm. Images: Richard Bateman.



et al. as ‘macrospecies’ and the 353 species recognised by Delforge as ‘microspecies’. Sandwiched between these two extremes are what I will here term ‘mesospecies’. For the sake of argument, the term ‘mesospecies’ can be taken to approximate the 23 groups into which Delforge (2016) aggregated his 353 microspecies, including the nine mesospecies that encompass the 113 microspecies supposedly encompassed by the single macrospecies *O. sphegodes* (viewed from a molecular perspective, *O. sphegodes* also encompasses such seemingly morphologically distinctive taxa as *O. reinholdii* and *O. bertolonii*).

I hope that employing these three terms to represent three contrasting hierarchical levels of *Ophrys* taxa (summarised in Figs. 2–10) will make the ensuing discussion easier to follow. Toward the end of this article, I will attempt to explain why maintaining three different hierarchical levels of taxa, all termed ‘species’, would be fundamentally unscientific.

***Ophrys* studies in the 2000s**

Building on earlier DNA-based studies, it was Devey *et al.* (2008) who finally put the cat firmly among the pigeons, having benefited from a one-off grant from the J.S. Lewis Foundation (yes, the famous department store chain!). Numbers of supposed species residing in the genus *Ophrys* had been steadily increasing for decades. Any underlying justifications offered for this proliferation of formal names by their authors relied on the subtlest of (usually poorly documented) morphological distinctions from other similar ‘microspecies’ and/or on observations of particular insect species interacting with particular *Ophrys* flowers (also usually poorly documented). Yet multiple DNA-based studies earlier in the decade had already shown that nuclear genes such as ITS and plastid genes such as *trnL-F* were unable to distinguish among this plethora of supposed species. In truth, Devey *et al.* could legitimately claim only two innovations relative to earlier DNA-based studies of *Ophrys*. Firstly, they applied three contrasting DNA-based analytical methods to plants representing a large number of microspecies. Secondly, on the basis of the data that they generated, Devey *et al.* were prepared to openly declare the fact that the emperor so obviously lacked substantial clothing, despite knowing that radically reducing the number of *Ophrys* species recognised would be a far from universally popular conclusion.

In a nutshell, two of the three DNA-based techniques applied by Devey *et al.* could resolve the *ca* 130 samples analysed into only six or seven distinct groups, and even the most discriminatory gene – nuclear ribosomal ITS – yielded only nine or at most ten groups. Each group was typified by a long-established, readily morphologically identifiable species (*insectifera*, *speculum*, *tenthredinifera*, *bombyliflora*, *fusca*, *apifera*, *umbilicata*, *scolopax*, *fuciflora* and *sphegodes*), the last three macrospecies proving barely separable from each other. In addition, despite strenuous efforts made to ensure that no hybrid plants were included in the study, several of the plants

analysed yielded multiple versions of the ITS gene, collectively providing good evidence that hybridisation between macrospecies had occurred within their recent genealogy.

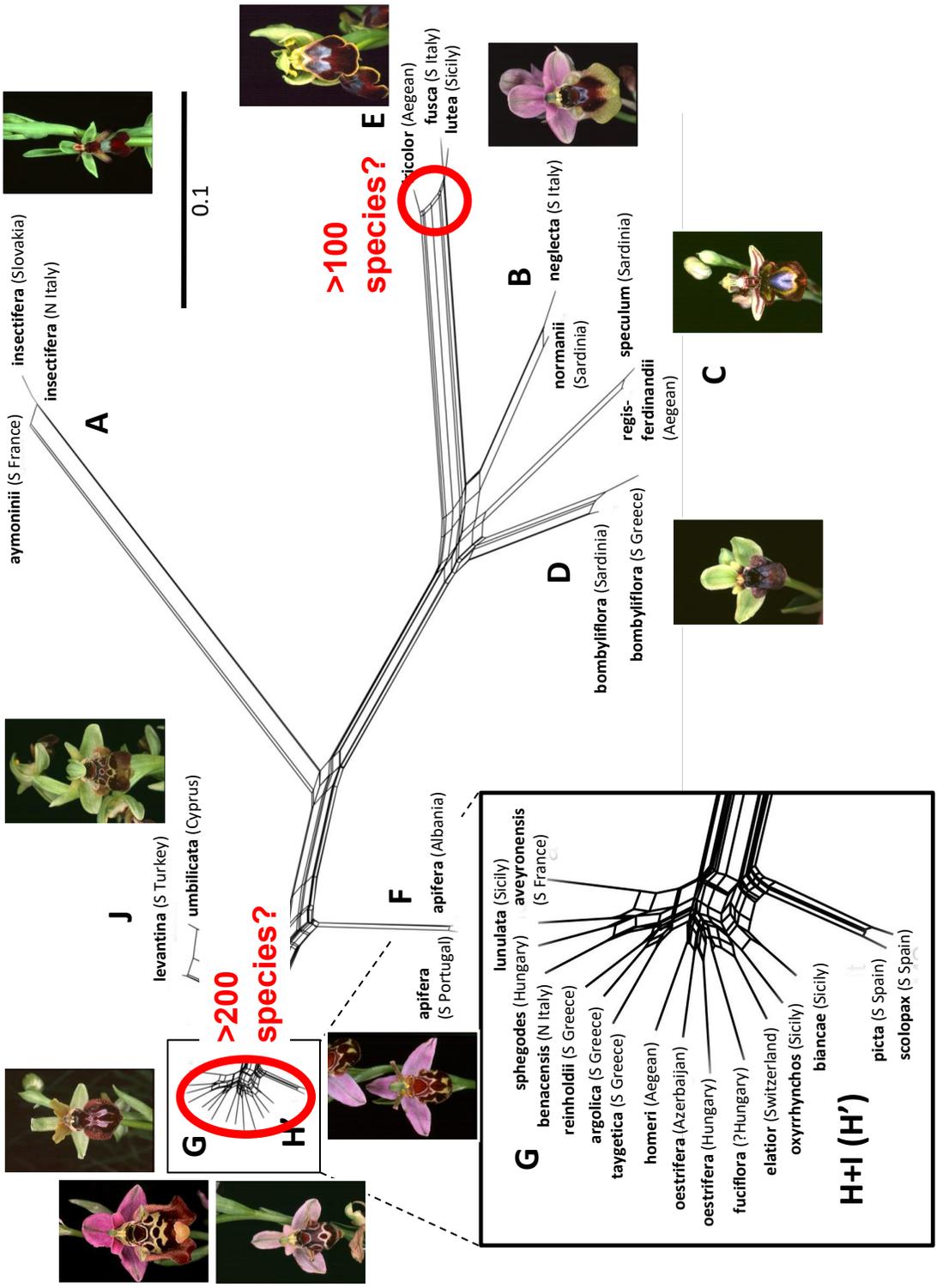
Although the failure of ‘candidate gene’ approaches to discriminate among *Ophrys* microspecies was in accord with the conventional wisdom that the genus is actively evolving, it also simultaneously contradicted frequent claims that the remarkable pseudo-copulatory pollination mechanism of *Ophrys* achieves a high degree of reproductive isolation. Artificial crossing experiments had already shown that any random pair of *Ophrys* taxa were likely to hybridise successfully following paintbrush-assisted transfer of pollinaria, but now the evidence of recent reproductive history recovered from ITS sequences had demonstrated that such gene-flow also occurs in nature. This realisation seriously challenged previous arguments that *Ophrys* microspecies each employ as pollinators a single (or at most, very few closely related) insect species (summarised by Paulus 2015). Thus, by the close of the 2000s, battle lines had been drawn between two schools of radically differing thought: geneticists relying primarily on the historical averaging of DNA to indicate greater gene-flow than is acceptable in stable, readily identifiable species (e.g. Bateman *et al.* 2011) versus ethologists still convinced that observations of interactions between particular flower morphologies and pollinating insect species are sufficient to infer recognition of yet another microspecies (e.g. Vereecken *et al.* 2011).

In practice, researchers subscribing to either of these two polarised worldviews (and indeed anyone holding compromise views) found themselves constrained by undesirably limited data. Was it reasonable for geneticists to draw general conclusions from DNA studies based on very few genes per genome and very few individuals per microspecies? Or for ethologists to rely on a small number of pollinator visits subjected to investigations very limited in time and space, and often pursued in a semi-artificial experimental system where plants and/or pollinators were deliberately moved around the natural landscape to increase the number of insect visits observed?

***Ophrys* studies in the 2010s**

Further progress was clearly essential. More recent European orchid studies have witnessed some geneticists taking advantage of new sequencing technologies, collectively termed ‘next-generation sequencing’ (NGS), that are designed to extract massively more DNA information from the plants analysed. Meanwhile, some ethologists are adopting a more sophisticated conceptual framework that better integrates multiple lines of analytical evidence and makes fewer prior assumptions regarding the likely outcome of the analyses.

Thus far, two of the three mainstream NGS techniques have been applied to *Ophrys*, though few of the results have yet been published. Each technique is capable of



generating one to at least two orders of magnitude more information than is generated during routine ‘candidate gene’ sequencing. Restriction-site associated sequencing (RAD) focuses on the nuclear genome. It was recently used to give a revised overall phylogenetic perspective on the genus *Ophrys* (Bateman *et al.* 2018), which is summarised here as Fig. 11. RAD also permitted a more focused study of the macrospecies *O. fuciflora* (Sramkó *et al.* in prep.), together with highly informative explorations of *Epipactis* (also requiring substantial reduction in the number of species recognised: Sramkó *et al.* submitted) and *Dactylorhiza* (Brandrud *et al.* in prep.). Genome skimming yields similar quantities of data but emphasises portions of genomes that are present as many copies in plant cells, including the entire plastid sequence (termed a plastome), nuclear ribosomal repeat regions such as ITS, and any viruses that have inserted themselves sufficiently firmly into the plant’s genomes. Within the last year this method has been applied to many microspecies within the macrospecies *O. sphegodes*, with results that are both intriguing and perturbing (Bateman *et al.* in prep.).

We could, for example, explore these massive new datasets simply by comparing the average genetic distances between different hierarchical levels. Let’s treat the average genetic distance between different populations of *O. cretica* as our basic unit. If we equate that basic genetic unit with a single mile and begin to journey northward from Trafalgar Square, that mile would take us only the length of Regent Street, as far as Oxford Circus. *Ophrys cretica* resides in Delforge’s *reinholdii* mesospecies alongside five other microspecies, including *O. reinholdii* itself (Fig. 5). Reaching *reinholdii* would move us 1.6 miles distant from Trafalgar Square, thereby allowing us to catch a Eurostar train at St Pancras station. The 3.0 mile distance to the mesospecies *O. sphegodes sensu stricto* would correspond with the fleshpots of Camden Town. Charting a course out of the macrospecies *sphegodes* and toward a nearby macrospecies, we would pass our first minor differences in ITS sequences before reaching *O. umbilicata* (Fig. 3) after a 6.6 mile journey, perhaps stopping to watch a match at Wembley Stadium. The much greater 44 mile distance to the most remote *Ophrys* macrospecies, *O. insectifera*, would lead us to the concrete cows of Milton Keynes. But in order to visit the closest genus to *Ophrys*, *Serapias*, we would have to travel all the way to the Scottish Border, 260 miles distant, passing approximately 120 ITS mutations en route. These figures emphasise the fact that members of the *Ophrys* clan are remarkably close-knit and inward-looking.

Fig. 11: Unrooted evolutionary tree of the genus *Ophrys* based on next-generation sequencing (RAD-seq), highlighting the nine reliably distinguishable macrospecies. Most of the presently-recognised microspecies diversity is encompassed in just two disparate regions of the tree: the *fusca* group, and the closely related *fuciflora* and *sphegodes* groups. Modified after Fig. 2 of Bateman *et al.* (2018).

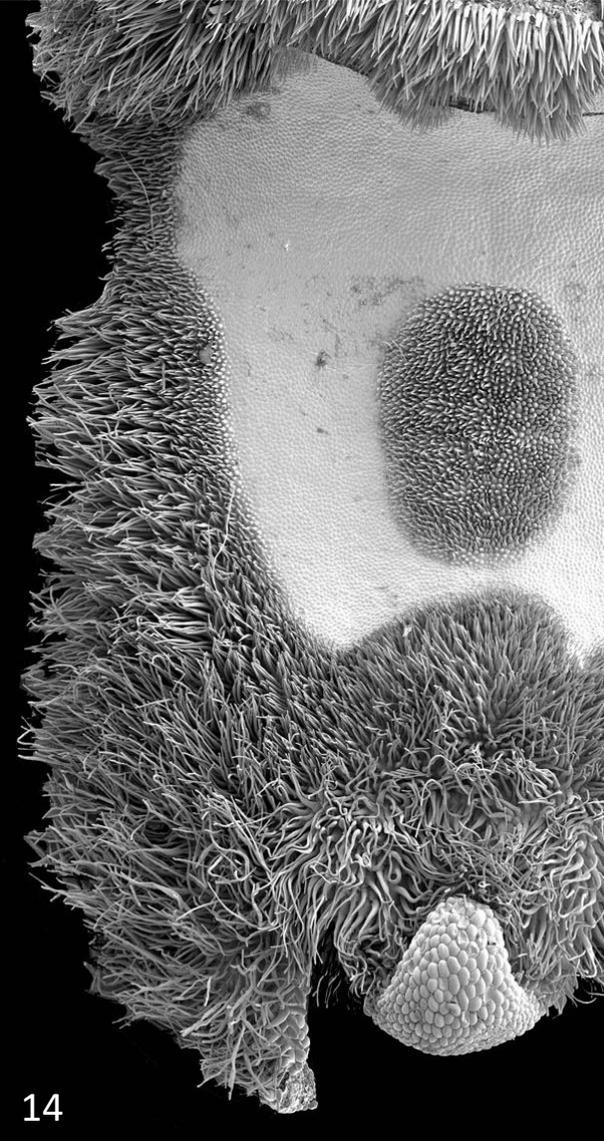
RAD analysis strengthened the evidence for previous conclusions regarding evolutionary relationships among the macrospecies but also made clear that, among mesospecies and microspecies alike, monophyly (evidence of a single evolutionary origin) was not going to emerge from so-called whole-genome data. Any remaining doubts on this matter have been laid to rest by whole-plastome genome skimming of the *sphogodes* group conducted during 2017, which has consistently revealed genetic differences between mesospecies and microspecies to be as great as genetic differences among different plants of the same microspecies. These results – not yet published – give timely reminders of a far more narrowly focused paper published four years ago by Sedek *et al.* (2014), presciently entitled “Genic rather than genome-wide differences [exist] between sexually deceptive *Ophrys* orchids with different pollinators.”

The study by Sedek *et al.*, and many others, have greatly enhanced our understanding of the remarkable features used by *Ophrys* plants to seduce pollinators (Figs. 12–15), first through pseudo-pheromone cocktails, then various visual attractants, and finally tactile stimuli. *Ophrys* has become *the* textbook case of pseudo-copulation. We have learned much about the biochemistry of the pseudo-pheromones, the micromorphology, physics and cell biology of the flowers, and behaviour of the insects (e.g. Paulus 2015). So much so that it is tempting to become seduced by such complex and elegant evolutionary products into ignoring the fact that pseudo-copulation is inherently a serious gamble, as it is the least efficient of all orchid pollination mechanisms (see Appendix 2 of Claessens & Kleynen 2011).

Hence, I would phrase the outcome of NGS research somewhat differently from the title chosen by Sedek *et al.* (2014): *Ophrys* microspecies appear to be the (in most cases transient) product of convergence of different populations toward generating similar pseudo-pheromone cocktails – cocktails that happen to appeal to a small number of closely related insect species capable of enacting (albeit comparatively inefficiently) pollination as a by-product of their febrile sexual appetites. If those

Figs. 12–15: Pollination and the three successive cues that draw a potential pollinator to an *Ophrys* flower: (12) Biochemical skeleton of the alkene (*Z*)-9-pentacosene, a significant component of the cocktail of pseudo-pheromones that first attract the insect toward the flower. (13) The complex and/or highly reflective labellar markings provide visual cues, epitomised by the highly reflective speculum of *O. speculum*. (14) Scanning electron micrograph of the labellum of *O. bertolonii* (*sphogodes* macrospecies), illustrating the remarkable complexity of epidermal cell types providing the tactile cues that mimic the body of a female partner. (15) The wasp *Argogorytes mystaceus* interacting with the labellum and gynostemium of *O. insectifera* in an apparent attempt at pseudo-copulation. Images: (13) Richard Bateman, (14) Paula Rudall, (15) Barry Tattersall.

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13



15



supposed species are still recognisable – morphologically and biochemically – in say 10,000 years’ time I would happily acknowledge them as bona fide biological species. But I predict (with the supreme confidence of someone who will not live to learn the accuracy of their prediction!) that most of today’s microspecies will be unrecognisable in just hundreds to thousands of years. Indeed, I would further reduce that estimate to just decades in the case of many highly localised ‘endemic’ microspecies that are actually merely hybrid swarms. Almost all of these transient lineages will soon be drawn inexorably back into their parental fold through gene flow. One or two may survive to eventually form fully fledged macrospecies, but how are we to identify which ones will be the winners? This is a challenge that would be rejected by any bookmaker, however long the odds being offered. Gene flow means that evolution within (rather than between) the nine macrospecies remains reticulate rather than divergent whenever and wherever physical constraints permit.

Given this scenario, the remarkable outcome is not that the genus *Ophrys* has somehow generated, in the blink of an evolutionary eye, at least 350 species to become the dominant genus in the European orchid flora (Delforge 2016). No, the remarkable outcome is actually that as many as nine macrospecies have somehow managed to achieve sufficient reproductive isolation through the last 2–6 million years to have evolved reliably recognisable genetic signatures (noting in passing the possible relevance of the catastrophic Zanclean Flood event that filled the former salt-pans of the Mediterranean Basin with seawater 5.3 million years ago). The long genetic branch that subtends the genus *Ophrys* without leaving any evidence of historical lineage divergence since its separation from the lineage that led to *Serapias* plus *Anacamptis* s.l. (an event that occurred an estimated 7–18 million years ago) tells me that we are not dealing with a case of recent and extensive speciation – a so-called evolutionary radiation – but rather are bogged down in a case of active microevolution that leads remarkably rarely to macroevolution (i.e. to *bona fide* speciation).

To summarise, the genus *Ophrys* is undeniably evolutionarily playful with its characters, not least with its pseudo-pheromones, but frankly, it has failed to become really serious about speciation. It is the orchidological equivalent of a teenager who has just discovered sex.

New challenges, old constraints

As orchid enthusiasts, we now find ourselves perched on an intriguing watershed. Broad-brush genetic analyses using next-generation sequencing (NGS) techniques can, when combined with sophisticated computer technology, provide us with vast bodies of data summarising the entire genome (or, more precisely, all three genomes: nuclear, plastid and mitochondrial). But at present, in order to make adequate sense of those data, you literally need to possess a PhD in information technology. And in

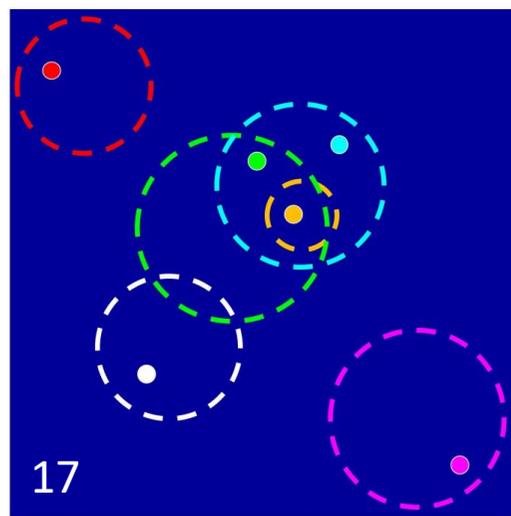
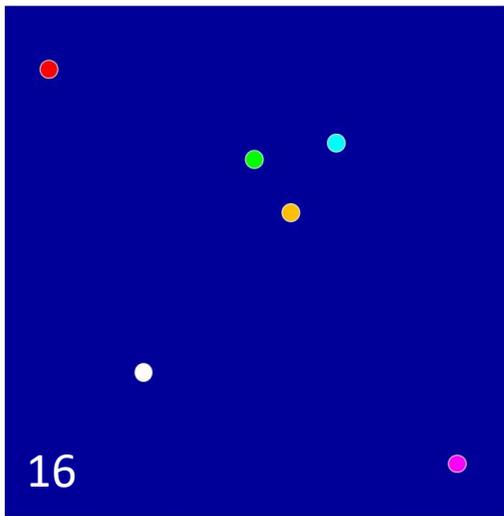
any case, the NGS data gathered thus far are proving incapable of reliably identifying not only *Ophrys* microspecies but also *Ophrys* mesospecies. Once you acknowledge that a well-trained chimpanzee could identify the nine *Ophrys* macrospecies without needing to resort to any scientific methodology beyond morphology-based intuition, the value of the much-vaunted resource-intensive NGS approaches appears open to question. Concurrent ultra-focused studies based on very few *Ophrys* populations are ably demonstrating one of the ways that *Ophrys* evolves – convergent biochemical mimicry of the pheromone cocktails of particular pollinating insect species – but they are incapable of demonstrating that this process leads to the formation of unambiguous species capable of independent existence in the longer term.

And at present, both broad-brush and ultra-focused approaches remain handicapped by two constraints. The first constraint is the amount of data currently available. The broad-brush approach has thus far generated too few whole-genome sequences to provide an adequate framework for species circumscription (and thus identification), whereas the ultra-focused studies have thus far explored insufficient populations to draw reliable generalisations. Secondly, both kinds of study tend to either under-explore or wholly ignore the morphology of the study plants, thereby being obliged to take as read (rather than seriously challenge) the formal microspecies names that we all use, most of which are the products of classical, essentially pre-scientific taxonomy. In the meantime, ‘classical’ taxonomists continue to describe new microspecies and infraspecific taxa of *Ophrys* with depressing regularity, usually on the basis of supposed (but inadequately demonstrated) subtle morphological differences from all other named taxa – the very characters that tend to be under-used by researchers using approaches that are more scientific in nature.

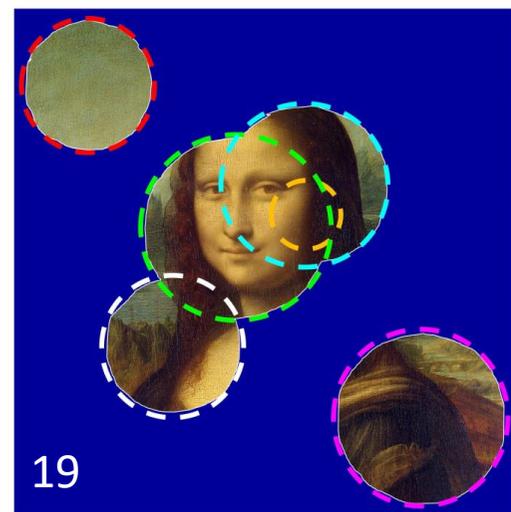
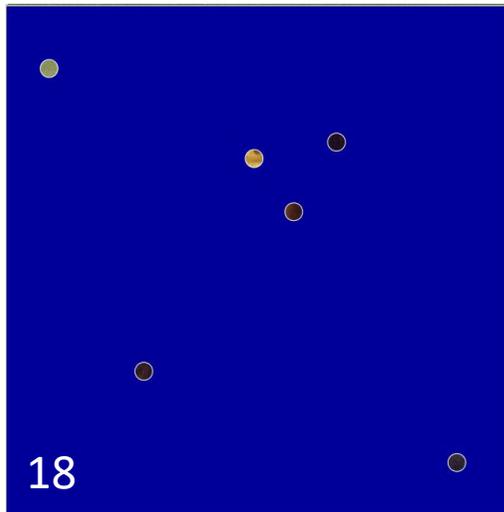
The drawing of conclusions from small quantities of information, requiring the radical assumption that the accumulated data are adequately representative of the organisms in question, is termed typology. At this point in the discussion, it is worth reminding ourselves of why typology is problematic. Fig. 16 shows six typological data points. Those data points could be the single type specimens deposited by classical taxonomists in herbaria to constitute the basis of all formal plant naming. Or they could be whole-genome DNA sequences extracted by systematic geneticists from particular named plants. Or they could be observations by ethologists of the interaction of a particular orchid with a particular pollinia-accumulating insect. In every case, the data point effectively constitutes a single observation.

If we then proceed to analyse, using the same technique as before, many plants from many populations of many closely related putative species, the true pattern eventually emerges in Fig. 17. The spheres of variation of four of those six putative taxa are shown to overlap, suggesting that, despite their subtle differences, these four taxa actually belong to the same species. In the case of the other two taxa, the

DNA/morphology/ecology



DNA/morphology/ecology



DNA/morphology/ecology

Figs. 16–19: Illustration of the crucial weakness of adopting a traditional typological approach to delimiting species. In (16), six type specimens have been used as the basis for formally establishing six species names. After much wider sampling that encompassed much of the variation present in those initial six presumptive species (17), we can see that four of the initial six specimens belong to the same species, so that only three credible species remain. In (18) and (19), a well-known painting had been placed beneath the data points; it is inevitably unrecognisable in (18), but readily recognisable in (19). Until evolutionary patterns become clear and reliable, any attempt to infer evolutionary process remains highly speculative.

original hypothesis that they are distinct species separated from all other species by discontinuities is upheld by the expanded data-set. Thus, relying on typological data is a gamble, albeit often a necessary one if resources are limited. Note how the typological observations in Fig. 18 are insufficient to reveal the identity of the famous painting placed behind the screen, whereas the much larger number of observations underlying Fig. 19 capture sufficient variation to allow instant identification of the underlying pattern.

Has systematic genetics reach its end-point?

I have repeatedly argued in print that a crucial part of the solution to the current ambiguous and hence controversial circumscription of species within *Ophrys* – and indeed within other orchid genera – is to place DNA technology in the hands of all natural historians (e.g. Bateman 2016), in the form of a long-awaited device that could generate DNA sequences in field conditions, immediately transfer those sequences via satellite to large publicly accessible databases such as GenBank, and thus provide an instant identification of the plant in question. Technology is at last moving in that direction, encouraged by rapid developments in NGS techniques but still with apparently an inadequate understanding by erstwhile developers of the potential scale of the market for such a device if it were to be made both affordable and user-friendly.

However, discussions of such devices are usually based on the assumption that their primary function would be identification. The common logic is that we would submit the results of a sample to GenBank and it would immediately offer us in return a prioritised list of names that represent the likely identity of the sampled plant. But in my opinion, this widely accepted scenario greatly under-estimates the likely value to science of placing DNA technology in the hands of all interested parties. That value actually lies in gradually eliminating typology, by greatly accelerating the rate at which DNA data are deposited in publicly accessible databases (Bateman 2016). At present, those databases are woefully inadequate for identification purposes, NGS data presently being almost non-existent. Only when DNA-based circumscription has at last been pursued to its logical conclusion will the potential of DNA to assist in the identification of orchids be adequately realised. At present, identifications all too often employ names of taxa that have no biological reality but are instead a construct of human imagination.

Unfortunately, the results of these earliest NGS studies now carry a worrying codicil. At the microspecies and even macrospecies level, *Ophrys* taxa are rarely if ever monophyletic (have a single evolutionary origin) when viewed through the prism of whole-genome data. Indeed, at any level below macrospecies, identification through DNA analyses will be a probability statement rather than a concrete evaluation. The fact that microspecies are not shown as monophyletic even when near-complete

DNA datasets are available suggests that similar morphologies and genotypes can originate on multiple occasions across Europe, and/or that gene flow from other macrospecies in the vicinity has occurred in the recent past. It is possible (though by no means certain) that large amounts of NGS data deposited in databases by us all in the near future would be sufficient to reveal such complicating factors and thus eventually lead to precise identification of biologically meaningful entities, not only applying a formal name to the plant in question but also revealing its reproductive and perhaps evolutionary history. At present, we simply do not possess the data needed to carry such discussions beyond the realm of mere speculation. Nonetheless, we are undoubtedly living in increasingly interesting times.

Species remain pivotal

Those readers who have courageously ploughed through this essay will likely by this point be wondering whether applying science to studies of the delimitation of species and the processes of speciation is sufficiently rewarding to justify the considerable effort involved. I admit that I increasingly feel as though I am the participant in a life-long game of slow-motion whack-a-mole. A classical taxonomist creates a name – typically a name based on very limited qualitative observations and unaccompanied by any explanation of what properties they believe a species should possess – and I must then spend years gathering the scientific data needed to determine whether that name actually has any scientific value (Bateman 2016). I have been obliged to reluctantly accept that I cannot compete with the short-cuts available to a traditional taxonomist. In practice, most of my DNA-oriented colleagues refuse to play the taxonomic game at all, understandably (but unhelpfully) arguing that their interest is in evolutionary processes and need not extend as far as the blood-soaked battleground of formal taxonomy. Unfortunately, if scientific data are not applied, formal taxonomy will continue to be practised as a dark art, and the resulting species will remain mere weak hypotheses of what might, or might not, be biological realities.

Having vented my frustration, I will now return to the distinction that I made at the beginning of this essay between genetically delimited macrospecies, ethologically and/or morphologically delimited microspecies, and the intermediate mesospecies that I initially regarded as the most intuitive and pragmatic level of species delimitation. For example, within the macrospecies *sphegodes*, accepting the mesospecies as the most intuitive of the three hierarchical levels would lump together such morphological subtleties as *O. spruneri*, *O. ferrum-equinum* and *O. gottfriediana*, but conversely would distinguish between seemingly more morphologically distinct species that contain *O. sphegodes*, *O. reinholdii* and *O. bertolonii* respectively. This potential solution would broadly reflect not only the “species groups” of Delforge (2016) but also the species recognised in the subspecies-dominated monograph of Pedersen & Faurholdt (2007). Superficially, emphasising mesospecies appears to offer an appealing compromise between the blindingly obvious macrospecies and

the head-scratchingly unidentifiable microspecies. Unfortunately, no dataset thus far gathered, nor any scientifically-based species concept thus far proposed, would allow the pre-eminence of mesospecies without ultimately resorting to taxonomic authoritarianism (also known as guesswork). As with microspecies, mesospecies appear to be an artefact of humankind's desire to classify and pigeonhole the self-generated chaos that is organismal diversity.

This unusually difficult situation is further exacerbated by the fact that in recent years the infraspecific ranks of subspecies, variety and forma have all diminished in usage, whereas these ranks would of course be crucial to any attempt to reclassify previously named *Ophrys* taxa within a more scientific framework – perhaps building on the preliminary work of Pedersen & Faurholdt (2007). But biology tells us that we cannot reasonably live in a world where three hierarchical levels are all referred to as species. Macrospecies, mesospecies and microspecies can exist together only as didactic tools; in practice, each of us must choose one of these three hierarchical levels. Conventional wisdom states that the species is the most self-definingly biological of all taxonomic ranks, perennially challenging us to decide conclusively which criteria must be fulfilled for a taxon to be widely recognised at species level. Will the real species *please* stand up?!

The broader context

I think it important to end by once again emphasising that the last few decades have witnessed a leap forward in our understanding of how *Ophrys* species, and orchids in general, function and evolve (consider, for example, the excellent synthesis produced by Claessens & Kleynen 2011). I will continue to argue that DNA-based analyses have had the greatest impact on orchid studies, particularly once their now pivotal role in identifying the partners in crime of orchids – mycorrhizae and pollinators – has also been taken into account. Nonetheless, research areas such as long-term demographics, mycorrhizal relationships and pollinator attraction have all yielded important insights. Life becomes even more interesting (though also even more complex) when multiple lines of investigation are combined into more multi-dimensional studies such as those of mixed-microspecies *Ophrys* populations pursued by Breitkopf *et al.* (2013) and Sedeek *et al.* (2014).

I will conclude by emphasising that the outcomes of temperate orchid research are not the sole preserve of scientists and natural philosophers but rather have immediate practical implications. For example, I am writing this article following a winter of unusual numbers of frost days and in the midst of the hottest, driest summer experienced in southern Britain for the last 40 years, which has impacted severely and negatively on the populations of many of our native orchid species. Accumulated data make it increasingly difficult for anyone to deny the existence of human-induced climate change. In a fascinating recent paper, Hutchings *et al.* (2018)



Fig. 20: Twelve plants that together provide a representative cross-section of the morphological spectra present in three populations of *O. sphegodes* sensu stricto in southern England. Horizontal dimension of all images = 22 mm. Images: Richard Bateman.

demonstrated convincingly that the flowering period of *Ophrys sphegodes* s.s. and the emergence times of the naïve males of *Andrena nigroaenea* (the orchid's most common pollinator) have diverged substantially through the last 356 years; both occur earlier, but the impact on bee emergence has been greater than that on orchid flowering. In other words, the Early Spider-orchid has become too (comparatively) late! The authors therefore advocated hand pollination, arguing that increasingly frequent summers of orchid–pollinator mismatches risk “complete reproductive failure” and could threaten the longer term survival of the orchid in England.

Hutchings *et al.* may well prove correct in their pessimistic assertion, if the hypothesis that each *Ophrys* microspecies is superbly adapted to pollination by just one bee species is true. However, it has already been proven untrue by Breitung *et al.* (2013), who found populations of *O. sphegodes* along the west coast of Italy to be visited more frequently by *Andrena bimaculata* than by *A. nigroaenea*. In this context, we should take into account the fact that approximately 67 further *Andrena* species are presently native to the British Isles. My prediction is therefore that although the peak flowering of the orchids may indeed have driven a wedge into a formerly beautiful pseudo-sexual relationship between *Ophrys sphegodes* and *Andrena nigroaenea*, that shift toward earlier flowering is also likely to be simultaneously driving the orchid into the arms of another – perhaps several other – *Andrena* bee species whose emergence will by chance have become more rather than less coincident with flowering of the orchid.

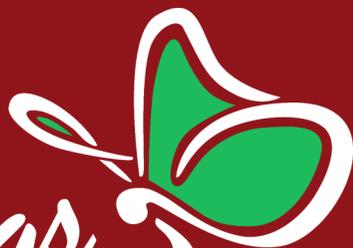
If my more optimistic scenario is valid, the wide geographic distribution of *O. sphegodes* s.s. across mainland Europe suggests that it is more likely to expand than contract its UK distribution if our summers are genuinely becoming warmer and our winters colder (i.e. more continental). I would also hazard a guess that the predilection of this species for disturbed calcareous habitats would allow it to exploit convenient avenues for northward expansion from our south coast along our chalk and limestone hills, thereby increasing the number of populations and total number of plants present in the UK. Given the subtle morphological differences already evident among *O. sphegodes* plants in southern England (Fig. 20), some of us may eventually become tempted to recognise and name multiple microspecies within British *O. sphegodes* populations. I hope that, by that point, we will *all* (literally) be better equipped to address such a challenge, and that DNA analysis will no longer be largely a spectator sport.

Acknowledgements. I am grateful to the many colleagues whose collective laboratory and IT skills have maintained my active involvement in DNA-based technologies into the 21st Century, notably Dion Devey, Gábor Sramkó, Ovidiu Paun and Oscar Pérez.

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Summer Disas on Table Mountain Peter Cowin

The Cape floral kingdom is well known for its sheer variety of plant life in a relatively small area of the globe. Inspired by several books, including two by W. P. U. Jackson; *Wild Flowers of Table Mountain* (1977) and *Wild Flowers of the Fairest Cape* (1980). I had long wanted to visit the area and did so for the first time in October and November 2008, but not principally to look for orchids. The South African spring was a revelation. We visited Cape Town and went up Table Mountain and the world-renowned Kirstenbosch Botanical Gardens, toured into the Little Karoo and travelled along the south coast Garden Route.

It was not until February 2017 that I was able to plan another trip to South Africa principally to visit the Drakensberg Mountains and also to fit in a few days in Cape Town in the hope of being able to see the summer flowering red Disa, *Disa uniflora*. In addition, the blue flowered *D. graminifolia*, and a third Disa, the orange-red *D. ferruginea*, should also be in flower at this time of year. Shortly before my trip I came across an excellent field guide; *Orchids of South Africa* (Steve Johnson & Benny Beitbier with photographs by Herbert Starker). There are about 470 species recorded in South Africa, the majority terrestrial, with a number of epiphytes in the warmer sub-tropical regions in the north and east. The genus *Disa*, having 143 species, is the largest with many having very restricted distributions. This book weighed in at a rather hefty 1.25Kg – I did not plan to use it in the field! It revealed the distribution of these three species. *D. uniflora* always grows with its feet in or close to water, relying on permanent streams to be able to grow. It is distributed around the Cape peninsula and north into the Cedarberg Mountains from sea level to 1450m, and described as ‘common’! The other two prefer drier conditions growing from 300-1500m, again around the Cape peninsula but also eastwards into the Langeberg.

We had allowed two days in or around Cape Town to search for these, with a planned trip up Table Mountain plus a day for an alternative location, the Fernkloof Nature Reserve. The latter is located on the edge of the coastal whale watching town of Hermanus, an hour’s drive east of Cape Town. As Table Mountain is often covered by mist (known appropriately as ‘the tablecloth’) the usual advice for planning a trip by cable car up Table Mountain is ‘if it’s clear go’! The afternoon we arrived was clear but uncharacteristically very windy which meant that the cable car was not running. The forecast for the following day was for the winds to moderate. The

Fig. 1: Spike of *Disa ferruginea*.
Fig. 2: *Disa ferruginea* in its habitat.
Fig. 3: Close-up of *Disa graminifolia*.
Photos by Peter Cowin



next morning proved to be equally windy, so in the hope of the following day being calmer we decided to drive out to Fernkloof, where according to the website, all three prospective Disas had been recorded. The reserve begins just to the north of the town at a modest elevation. We would need to do some uphill walking to get to higher elevations where we might find them. We set off optimistically and got to an elevation of 500m where there were several permanent streams running through much drier stony hillsides. A number of flowers were seen including a pretty gladiolus, several heathers and some orange flowered bulbs, this was despite a severe drought in the Western Cape, but after 3.5 hours walking no sign of any Disas! The few permanent streams seemed to have too much dense shrubby vegetation around them to allow *D. uniflora* to grow, nor was there any sign of the other two species in the drier open hillsides. Hopefully, the next day would allow us to go up Table Mountain, if the wind subsided.

Fortunately, the next day dawned clear and almost windless. We got to the cable car station at 9:00 to find that the previous two days closure of the cable car had led to a huge pent up demand and the queues were depressingly long. However, we were fortunate to find a couple of people in the queue who had tickets but decided they did

not have time to go up as they had to be at the airport to fly back to Europe. So, after a much shorter wait than we expected we got to the top at 1000m. There were large numbers of visitors near the top station, where a number of concrete paths lead to various view-points close to the cable car station. These paths are discretely fenced to discourage people wandering over the low, fragile fynbos vegetation. Our planned walk took us along the relatively flat ‘top table’ from where we would need to head down into one of the valleys of the ‘back table’ to be able to find a permanent stream.

After only a few minutes I spotted a single *D. ferruginea* with its dense spike of relatively small vivid orange-red flowers, it was a good 10m away from the path, so we continued on soon spotting another, this time quite close to



Fig. 4: Spike of *Disa graminifolia*.

Fig. 5: Close-up of *Disa graminifolia*.

Fig. 6: *Disa graminifolia* in its habitat.

Photos by Peter Cowin

5



6





the edge of the path. While photographing this I was aware of someone behind me excitedly talking to a friend about the blue Disa. I turned to see him examining several spikes of the true-blue flowers held well above the surrounding low vegetation. The individual flowers 2.5-3cm across were well spaced along the spikes with 2-3 open on each. The hooded flowers had clear gentian blue sepals and petals, only the lip was a more violet hue with two clear green lobes on the upper apex of the petals. Blue is that rarest of colours in the orchid world! Walking on further, more spikes of both *D. graminifolia* and *D. ferruginea* were evident dotted here and there including a couple of *D. graminifolia* on which the lips were closer to blue rather than the more usual violet.

The blue Disa is pollinated by carpenter bees. This is unlike the red or orange flowers of *D. ferruginea* and *D. uniflora*; these are pollinated by a butterfly known as the Mountain Pride which is strongly attracted to this colour. We saw this large two-tone brown butterfly quite frequently but none in action on the Disas. From below in Cape Town Table Mountain does indeed look very flat but once at the top the topography is revealed to be more complex. To the south, the ‘back table’, there is an overall reduction in elevation with the plateau crossed by several valleys running east/west. It is these that hold permanent streams. Some of these have been dammed over the years to create reservoirs which still supply a small proportion of Cape Town’s fresh water. It was down into the first, Echo Valley, that we wanted to descend to the stream in the hope of finding *D. uniflora*. As we descended many plants and flowers caught the eye including the magnificent king protea, *Protea cynaroides*, just beginning to flower. As we descended towards the valley floor a couple of bridges crossing the stream could be seen at a distance of 2-300m. Could we detect some splashes of red? Down at stream level the first crossing revealed several flowers of *D. uniflora*, their large 10-12cm wide flowers held on 30-50cm stems above the banks of the slow-moving stream. Here the peaty stream banks were about 50-60cm high and almost vertical with numerous vegetative plants of *D. uniflora* growing just above the water line, showing that relatively few were producing flowering stems. This made photography somewhat awkward as the flower stems tended to arch out over the water. The path led on running parallel to the stream, the red flowers being apparent here and there all along the banks. So, after the disappointment of the previous day, Table Mountain had been the place to see, relatively easily, plenty of specimens of these magnificent orchids.

Fig. 7: *Disa uniflora* in its habitat.

Fig. 8: Close-up of *Disa uniflora*.

Photos by Peter Cowin

Funny Things These Bees Alan Smith

Variations in Bee Orchids seem to have received more attention than in other species and names have been established for many of them. Apart from these named variants, other unusual plants exist, and 2018 has been a bumper year for them. Eight such plants are described and illustrated below, the made up names are for amusement only.

Badensis Trollii [illustrated on the rear cover]: These are of course established names but by definition, *badensis* must have a normal *O. apifera* lip, and *trollii* normal *O. apifera* petals; that being the case neither apply to this plant. However, with the sepaloid *badensis* type petals and *trollii* style lip I think it describes it pretty well. Perhaps this opens up a whole new plethora of possibilities for plants with features from more than one named variant.

Botteronii(ish) [Figure 1]: As far as I'm aware *botteronii* has only appeared very infrequently in the UK and is characterised by having sepaloid petals and an asymmetrical pattern on the lip. The lip pattern on this one appears to fit the bill and the petals are certainly large and unusual. Long enough and sepaloid enough? Perhaps not, but not a bad attempt.

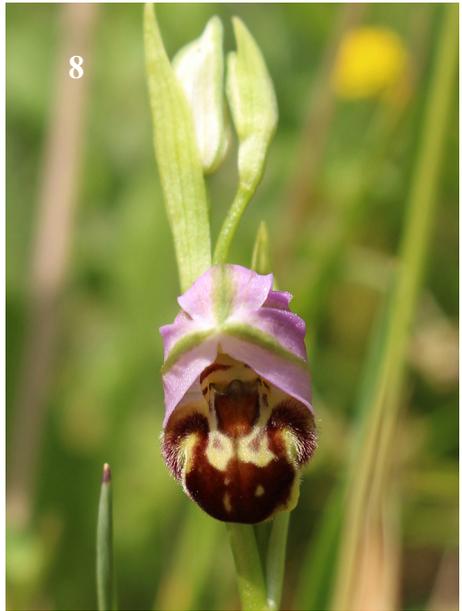
Crikey [Figures 2 & 3]: I didn't have to think of a name for this one, it just came out of my mouth when I set eyes on it. Two photographs for this one, a single shot wasn't enough to illustrate it very clearly. Flowers with just four perianth segments are seen from time to time on *Ophrys apifera* as well as other orchid species, but the nature of the petals on this one seemed especially unusual. The petal on the right looks like an attempt at the left side of a normal lip complete with side lobe, and *vice versa* the left petal. Funny things these bees!

Geminii [Figure 4]: When first noticed this one appeared to be producing two overlapping lips but that is not the case. The lip as you see it in the photograph is exactly what it is, a nice attempt at twins.

Peculiarity [Figure 5]: Perhaps the most peculiar of the bunch. Apart from this flower, the plant was a normal *trollii*, and the right hand side of this flower is also normal *trollii*, but as you can see from the photo, the left side of the flower is anything but normal. The lip on this side is attempting to be peloric, and something I don't remember ever seeing before, the remarkably long petal on the left is fused to, and replacing the top half, of the lateral sepal. All this leaves a very peculiar flower with just five perianth segments.

Teensy [Figure 6]: In spite of how it appears on the photo, the 10p coin is actually resting right back against the lateral sepal; this was a normal sized plant with tiny flowers. A few orchid species have named variants with small flowers but this seems not to be the case with Bee Orchids. At 7mm long the lip is about 60% of the size of an average *O. apifera*, and rather surprisingly, there were a number of similar plants close by.





The last two, **Snugly** [Figure 7] and **Turbanii** [Figure 8], are just a bit of fun with sepals behaving badly. Nice to see but probably just drought victims with flowers failing to open properly.

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