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General Discussion

The present work brings together the results of systematic, phylogenetic and pollination studies of orchid species belonging to the genus *Specklinia*, with special emphasis on those with a Costa Rican distribution. It is organized in three distinct sections that contain manuscripts of similar topics for ease of the reader.

Contributions towards our systematic knowledge of *Specklinia*:—This section focuses on the systematics of *Specklinia* species by treating groups of closely related and badly understood species systematically.

The first group to be dealt with is that of the *Specklinia endotrachys* species complex. Traditionally considered a morphologically variable species, *S. endotrachys* is here treated as one of six distinct, albeit closely related, taxa. Four species were originally recognized in chapter 1, and two more are added in chapter 2. Of those species, *S. pfavii*, and *S. spectabilis* are described and illustrated from living material and removed from the synonymy of *S. endotrachys*, while *S. dunstervillei* and *S. remotiflora* are described as new to science.

The second group to be addressed is that of the *Specklinia glandulosa* species complex. Traditionally, and similar to the previous case, *S. glandulosa* has been considered a variable species along its broad range from Mexico to the Guiana Shield. In chapter 3 it is found to be one of at least six different, morphologically and ecologically similar, but well distinguished, species. Of those species, *S. pertenuis* and *S. vittariifolia*, are reconsidered and removed from the synonymy of *S. glandulosa*, while *S. alajuelensis* and *S. gersonii* are described as new to science. *Specklinia chontalensis* is described and illustrated from Costa Rican material.

In chapters 4 and 5 two single new species of *Specklinia* are described. In contrast with the species discussed in the previous chapters, these have not been confused with other similar species. In chapter 4 the very unique (even absurd) *Specklinia absurda* is described. It was discovered recently by the authors in the seldomly explored mountains of the Costa Rican south-Pacific. In chapter 5 the *Specklinia lugduno-batavae* is described. This tiny, creeping plant from the Caribbean lowlands of Costa Rica apparently had escaped previous collectors. The name honors Leiden University and the Hortus botanicus Leiden.

After the publication of these papers disentangling the mentioned species' complexes it became obvious that the species treated here are quite different. At the time we wondered why they were considered a variable, yet single, species for so long? The answer now seems to be straightforward, when similarities appear much larger than individual differences, we tend to overlook those differences. With little material at hand we find ourselves unable to adequately assess intra- and inter-specific variation. With more material for study it is possible to finally understand that even though our species' have certain similarities that set them aside from other species, they also have differences from each other. It is important to use all the evidence possible, linking morphology, ecology and molecular data, in order to avoid seeing things that are not there. It is important to point out that if we stare too long at copies of the same thing we will eventually find differences between them.

Phylogenetic reassessment of *Specklinia* and its allied genera:—After the publication of the first molecular phylogeny of the Pleurothallidinae many species were transferred to genus *Specklinia*. In the last decade different authors have assigned 40 to 420 species to the genus. In chapters 6 and 7 we re-circumscribe the genus in order not only to establish how many and which species belong to it, but also how they can be recognized both morphologically and ecologically.

We find that about 95 species belong to *Specklinia* in the broad sense, and that this includes the type species of the genera *Acostaea*, *Arelidia*, *Cucumeria*, *Empusella*, *Gerardoa*, *Pseudoctomeria*, *Sarcinula*, *Sylphia*, *Tribulago* and *Tridelta*, which are therefore here considered synonyms of the first. Alternatively, *Specklinia* would be reduced to just a few species and quite a few additional generic names would require recognition. Taking into consideration that *Specklinia* in a broad sense is monophyletic with the removal of *Muscarella*, that it is manageable in size, and that it can also be easily recognized morphologically, it seems unnecessary to recognize those splinter generic concepts. *Specklinia* has a north-Andes to south-Central America speciation pattern. On one hand, even though the genus has an overall wide distribution, ranging from Mexico to Bolivia and Brazil, through Central America and the

Antilles, the highest species and clade diversity is found south-Central America. On the other hand, its sister taxa *Platystele*, *Teagueia* and *Scaphosepalum*, as well as their sister *Muscarella*, are most diverse in the north-Andes. The relatively young age of both geographical locations indicates that the diversification of the entire clade must have happened quite recently. Ongoing molecular clock studies are currently providing more insight in this.

Incaea, a monospecific genus that was previously unplaced, is here found embedded within *Dryadella* and synonymized. The also unplaced and monospecific *Rubellia* is found sister to *Platystele* and reduced as a synonym. *Teagueia*, which is morphologically similar to *Platystele* and from which it was segregated recently, was unexpectedly found sister to *Scaphosepalum* instead. The phylogenetic position of a group of species with “*Specklinia*-like habit and *Anathallis*-like flowers”, and which have been going back and forth between both genera is finally resolved. They are segregated into the new generic concept proposed here, *Lankesteriana*. This name honors Lankester Botanical Garden and its scientific journal.

The superficial morphological dissimilarities among species of *Specklinia* led to a proliferation of generic concepts, proposing the segregation of several small species groups from the genus. Nevertheless, we have been able to show that *Specklinia* as here defined is monophyletic and can be recognized by several morphological characters that had not been considered before. Some of the taxonomic decisions presented in both chapters are likely not to be accepted unanimously, and indeed these are nothing but proposals based on the data available and our best interpretative capabilities. They are not sculptured in stone, and might eventually be trumped by newer techniques and evidence. In the meantime, without contradicting data a critique is nothing more than an opinion.

Assessing the pollination mechanisms of *Specklinia*:—The first documented observation of pollination in Pleurothallidinae was that of Augustus Endrés who noticed that the “viscid sepals” of *Specklinia endotrachys* were visited by a “small fly”. Mark Chase would later identify the visiting flies as being of the genus *Drosophila*. In chapter 8 we document and describe how species of the *Specklinia endotrachys* complex are pollinated by different *Drosophila* species.

We found that *Specklinia endotrachys*, *S. pfavii*, *S. spectabilis* and *S. remotiflora* are pollinated by up to 13 different species of the *Drosophila*, especially of the *D. repleta* group. Several unrelated genera of Pleurothallidinae, including *Acianthera*, *Dracula*, *Masdevallia*, *Specklinia* and *Stelis* (in a broad sense), have species that share a similar system in which pollinia removal occurs when a fly is pushed against the column once it walks over the lip; whilst exiting in reverse, the pointed scutellum is smeared with a viscid substance found in the rostellum, and the pollinia are removed by touching their twisted base. In those genera the observed pollen removal is reported to occur mostly by flies of the families Chloropidae, Drosophilidae and/or Phoridae. It is thus essentially how the fly is guided to visit the column/lip cavity that differs between these different pleurothallid species’ groups.

We showed that species of the *S. endotrachys* complex arrest the flies using aggregation pheromones, including ethyl tiglate, methyl tiglate and isopropyl tiglate. Pheromones are likely to play an important role in initially aggregating Diptera species on pleurothallid flowers. Here we have been able to confirm for the first time that aggregation pheromones are being released from the sepals of *Specklinia* species to attract pollinators. The pollinators showed frequent courtship behaviors even though they rarely copulated on the flowers. The use of pheromones, be it sexual or aggregation, might be generalized in Pleurothallidinae considering that a wide range of species have secretory structures. Scent is likely to play an important role in specific pollinator attraction thus mediating reproductive isolation, and nothing is more convincing than pheromones.

Visible nectar drops on the adaxial surface of sepals of these *Specklinia* species are secreted from nectar secreting stomata. These encourage the *Drosophila*, both males and females, to linger on the flowers for several hours at a time. Nectar guides are also commonly used by pleurothallids to guide the pollinators to the lip/column cavity. Many studies seem to report no “measurable” or “obvious” rewards, however evidence for nectar guides is frequently found in more detailed pollination studies in the pleurothallids. The appearance of nectary glands has been found to lead to an increase in reproduction success. Pollination efficiency was found to be significantly lower in food deceptive orchids as compared to rewarding species, and several authors have suggested that deceitful species must occur much less frequent than rewarding ones otherwise the evolution of lack of reward is difficult to explain. In fact we wonder if the cases in which orchids are being considered non-rewarding are not highly over-estimated, as absence of evidence is not evidence of absence.

A look into the future:—There are most likely more than 7000 species in subtribe Pleurothallidinae, several hundreds patiently awaiting discovery. The vastness of the subtribe allows for endless research opportunities, but it is also a tremendous challenge. Entire lineages were completely unknown until only a few years ago, and many are probably still unknown today. The alpha-taxonomy, the discipline of detecting, describing and classifying species, is still badly needed to set a strong base for evolutionary interpretations within the pleurothallids. Nevertheless, the future looks bright. The knowledge on species belonging to the group has had an exponential growth since the publication of the first modern monograph of Pleurothallidinae three decades ago. Luckily even though scientist are ephemeral, scientific knowledge lingers.

Floral morphology is immensely diverse in the subtribe suggesting a plethora of different pollination syndromes employing modifications of the deceit/reward system. Judging by the numerous cases of convergence in flower morphology it is highly likely that the employment of pheromones (both sexual and aggregation) arose several times independently in the subtribe. The adaptation to the same pollinator groups (such as Drosophilidae) by several unrelated groups of Pleurothallidinae strongly suggests cases of parallel evolution. In the future, with the pollinators of more pleurothallids being documented, we will be able to apply molecular dating techniques in order to establish whether these orchids and insects have radiated synchronically, or if, which is more likely considering their relatively young age, the pleurothallids exploited the preexisting fly diversity. Advances in the genome data will help unravel how aggregation and sex pheromones evolved in the Pleurothallidinae. Full genomes of orchids are nowadays being assembled with more frequency, for example the nuclear genome of the Costa Rican *Erycina pusilla* (L.) N.H. Williams & M.W. Chase, a deceptive orchid, is being assembled in a few labs around the world, including Leiden. Genome data will also allow to identify genes or groups of genes with accelerated evolutionary rates, which is key in understanding how so many Pleurothallidinae species could radiate in such a short evolutionary time.

The high diversity in the pleurothallids may also have potential practical uses. The flowers of these orchids are specialized in the attraction of a diversity of flies, many of which are serious agricultural plagues. As shown here, *Specklinia* species aggregate a diversity of *Drosophila* species employing aggregation pheromones. Some species of *Drosophila*, such as *D. suzukii*, are well-known greenhouse pests and it is likely that they too can be aggregated with certain pheromones. A pleurothallid-based pheromone dispenser would be an exciting and innovative alternative to the use of other chemical controls.