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1. GIVEN NAMES AND SURNAME: Marta Alicja Kolanowska

2. ACADEMIC DIPLOMAS, DEGREES – name, place and year of obtaining

- 2012, Gdańsk University of Gdansk - Post-graduate studies in Forensic Biology  
Dissertation title: The role of botanist in identifying and indicating the origin of the cannabis derivative drugs
- 2012, Gdańsk University of Gdansk, Faculty of Biology - PhD studies in Biology, Ecology and Microbiology  
Thesis title: Taxonomic diversity and geographic distribution of Orchidaceae species in the Colombian department of Valle del Cauca
- 2009, Gdańsk University of Gdansk, Faculty of Biology - Master's degree  
Specialization: environmental biology  
Dissertation title: Morphological and genetic variation within populations of *Dactylorhiza incarnata* (L.) Soó (Orchidaceae) in the selected areas of Gdansk Pomerania

3. ACADEMIC EMPLOYMENT AND PROFESSIONAL EXPERIENCE

- since 9 X 2012 Assistant professor in the Department of Plant Taxonomy and Nature Conservation, University of Gdansk
- VII 2013, VII 2012, X 2010, VIII 2011, Metaplantation of *Epipactis helleborine* (Orchidaceae) from the Gdynia-Kosakowo airport and monitoring of the metaplanted population
- VII 2010, X 2009 Metaplantation of *Epipactis atrorubens*, *Epipactis helleborine* and *Eryngium maritimum* from the projected breakwater in Westerplatte
- V-IX 2010 Participation in the project „Conservation of the coastal resources of *Eryngium maritimum* and assessing the impact of tourism activities in the Mechelińskie Łąki Nature Reserve”

4. SCIENTIFIC ACHIEVEMENT (AS INDICATED IN ART. 16 SEC. 2 OF THE ACT FROM 14 MARCH 2003 ON THE ACADEMIC DEGREES AND THE ACADEMIC TITLE AS WELL AS ON THE DEGREES AND THE TITLE WITHIN THE SCOPE OF ART (D. U. NO. 65, POS. 595, AS AMENDED)

4A. Title of the scientific achievement

**Bioclimatic niche modeling as a tool for biogeographic research on Orchidaceae**

4B. List of publications constituting the scientific achievement

	<b>Publication</b>	<b>MNiSW score</b>	<b>IF</b>
H1	Kolanowska M. 2013. Niche conservatism and the future potential range of <i>Epipactis helleborine</i> (Orchidaceae). PLoS ONE 8(10): e77352 (DOI:10.1371/journal.pone.0077352).	40	3.534
H2	Kolanowska M. 2013. Glacial refugia and migration routes of the Neotropical genus <i>Trizeuxis</i> (Orchidaceae). Acta Soc. Bot. Pol. 82(3): 225-230 (DOI: 10.5586/asbp.2013.024)	20	1.195
H3	Szlachetko D.L., Górniak M., Kolanowska M., Mytnik-Ejsmont J., Kowalkowska A., Rutkowski P., Koliński T. 2014. Taxonomic position and phylogeny of the genus <i>Vargasiella</i> (Orchidaceae, Vandoideae) based on molecular and morphological evidence. PLoS ONE 9(6): e98472 (DOI:10.1371/journal.pone.0098472)	40	3.534
	<i>Contribution: 20%</i>		
H4	Kolanowska M. 2014. The naturalization status of African Spotted Orchid ( <i>Oeceoclades maculata</i> ) in Neotropics. Plant Biosystems 148(5): 1049-1055 (DOI: 10.1080/11263504.2013.824042)	25	1.91
H5	Kolanowska M., Konowalik K. 2014. Niche conservatism and future changes in the potential area coverage of <i>Arundina graminifolia</i> , an invasive orchid species from Southeast Asia.	25	2.084

	Biotropica 46(2): 157-165 (DOI: 10.1111/btp.12089)		
<i>Contribution: 50%</i>			
H6	Kolanowska M., Szlachetko D. L. 2014. Niche conservatism of <i>Eulophia alta</i> , a trans-Atlantic orchid species. Acta Soc. Bot. Pol. 83(1): 51-57 (DOI: 10.5586/asbp.2014.007)	20	1.174
<i>Contribution: 90%</i>			
H7	Kolanowska M. 2014(2015). Determination of potential glacial refugia and possible migration routes of <i>Campylocentrum</i> (Vandaeae, Orchidaceae) species through the Darién Gap. Acta Soc. Bot. Pol. 84(1): 97-102 (DOI: 10.5586/asbp.2014.030)	20	1.174
H8	Naczek A., Kolanowska M. 2015. Glacial refugia and future habitat coverage of selected <i>Dactylorhiza</i> representatives (Orchidaceae). PLoS ONE 10(11): e0143478 (DOI: 10.1371/journal.pone.0143478)	40	3.534
<i>Contribution: 50%</i>			
H9	Kolanowska M., Mystkowska K., Kras M., Dudek M., Konowalik K. 2016. Evolution of the climatic tolerance and postglacial range changes of the most primitive orchids (Apostasioideae) within Sundaland, Wallacea and Sahul. PeerJ 4:e2384 (DOI: 10.7717/peerj.2384)	35	2.183
<i>Contribution: 40%</i>			
H10	Kolanowska M., Naczek A.M., Jaskuła R. 2016. Herbarium-based studies on taxonomy, biogeography and ecology of <i>Psilochilus</i> (Orchidaceae). PeerJ 4:e2600 (DOI: 10.7717/peerj.2600)	35	2.183
<i>Contribution: 70%</i>			
<b>MNiSW score: 300</b>			
<b>Total IF: 22.505</b>			

#### 4C. Overview of the scientific achievement (H1-H10)

Orchidaceae is one of the most diverse, cosmopolitan family of Angiosperms that includes about 27000 species representing 730-880 genera (Pridgeon et al. 1999, 2001, 2003, 2005, 2009, 2014, Chase et al. 2015). Despite considerable interest of scientists in studies on orchids, numerous aspects of biology and ecology of these plants remain unknown.

The essential gap in the current knowledge is historical biogeography of Orchidaceae which is a result of substantial lack of palaeobotanical data. Orchid fruits contain hundreds of thousands of seeds that lack an endosperm. Those have not been detected in the fossil material so far. Also macroremains of Orchidaceae, non-lignified stems and leaves that are often devoid of sclerenchyma, are rarely traced by palaeobotanists. This is related to the general distribution of orchids. The highest diversity of species is observed in tropical areas that are characterized by the rapid decomposition of organic matter. So far the leaves of just two orchid genera, *Dendrobium* Sw. and *Earina* Lindl. (Conran et al. 2009) were identified in fossil material. Indirect footprint of those plants, pollen-bearing insect, preserved in amber was described by botanists from Harvard University in 2007 (Ramírez et al. 2007). Insufficient palaeobotanical data limited studies on the history of Orchidaceae, especially in terms of their post-glacial migration.

Another obstacle in the research on orchids is related to the significant deficiency in the information about their ecology, especially habitat requirements of tropical taxa. Difficulties in gathering data on their preferred niches have so far limited studies on the impact of future climatic changes on their potential distribution which is crucial for establishing long-term nature conservation plans, e.g. selection of areas which should be monitored, designed as protected by law or estimating expansion ranges of invasive plants. First comprehensive mathematical models of future climatic changes were developed in the mid-XX century, but their usage is possible only for taxa with recognized ecological tolerance, or at least climatic niche requirements. For this reason these models were not used in studies on Orchidaceae.

Moreover, the lack data on the habitat and climatic preferences of orchids preclude any studies on the evolution of their climatic tolerance and phylogenetic niche conservatism (PNC). The concept of PNC which is one of crucial aspects of evolution, was intensively

discussed by ecologists and taxonomists (e.g. Harvey & Pagel 1991, Price 1997, Harvey & Rambaut 2000, Ackerly 2003, Losos 2008, Cavender-Bares et al. 2009). The tendency of a species to retain ancestral ecological characteristic (Wiens & Graham 2005) was impossible to evaluate due to the lack of a techniques allowing characterization of the ecological niche of the organisms. The situation changed when the environmental niche modelling applications became available (e.g. Guisan & Zimmermann 2000). These programs became useful tools also in phylogenetic studies (e.g. Marske et al. 2011, Bond 2012). Despite improvement of molecular techniques in the studies on Orchidaceae, PNC was not studied within these plants due to the lack data on their habitat requirements.

The aim of my research was to adapt ecological niche modeling (ENM) applications based on presence-only data (MaxEnt, Philips et al. 2004, 2006, Elith et al. 2011) and the analytic tools (ENMTools, Warren et al. 2010) to the biogeographic studies on Orchidaceae. Analysis was devoted to the fundamental aspects of plant phytogeography, such as distribution of glacial refugia, post-glacial migrations and potential range modifications related to climate changes, with special respect to invasive taxa. Furthermore, using the ENM methods I conducted research on the phylogenetic niche conservatism of the most primitive Orchidaceae

### **ENM in studies of invasive species**

- Kolanowska M. 2013. Niche conservatism and the future potential range of *Epipactis helleborine* (Orchidaceae). PLoS ONE 8(10): e77352.
- Kolanowska M. 2014. The naturalization status of African Spotted Orchid (*Oeceoclades maculata*) in Neotropics. Plant Biosystems 148(5): 1049-1055.
- Kolanowska M., Konowalik K. 2014. Niche conservatism and future changes in the potential area coverage of *Arundina graminifolia*, an invasive orchid species from Southeast Asia. Biotropica 46(2): 157-165.

The invasive species are uncommon among Orchidaceae and only 90 species are listed in „Global compendium of weeds”. The nature of the expansion of those plants into new areas

remained unexplored for years. My studies concerned three species: *Epipactis helleborine* (L.) Crantz, *Oeceoclades maculata* (Lindl.) Lindl., oraz *Arundina graminifolia* (D. Don) Hochr.

The first one, that occurs also in Poland, is an invasive element of North American flora. *Epipactis helleborine* in the native range occurs in deciduous forests, coastal dunes as well as in the anthropogenic habitats. For the first time the occurrence of this species in the United States was reported in 1879. Its expansion in North America intensified in the 30' of XX century. Molecular studies did not indicate significant genetic differences between invasive and native populations (Squirrell et al. 2001). For years it was believed that the occurrence of *E. helleborine* on both coasts of the United States is associated with the structural similarity of the local forests to Eurasian vegetation (Adamowski 1995).

In this study [H1] the database of *E. helleborine* localities was divided into native and invasive sets. To compare the geographical distribution of the suitable niches for both groups the range overlap indexes were used and to evaluate the similarity of the occupied niches Schoener's D, I and RR statistics were applied (Warren et al. 2010). Three separated analysis were performed. The 1<sup>st</sup> one included all known localities of *E. helleborine* and the other two based on native- and invasive-only data. The contribution of climatic factors (Hijmans et al. 2005) was calculated for all three models. For the analysis of the future range modifications in 2080 (Ramirez & Jarvis 2008) all occurrence records of *E. helleborine* were used. The possible modification of potential range related to the future climate changes were evaluated for three scenarios A1b, A2a, and B2a (Intergovernmental Panel on Climate Change 2000).

Maps of the suitable niches distribution varied between the three models created for the present time. The model based on all available data indicated central and western Europe, including the British Islands as well as Norway and Iceland as the areas of potential range of *E. helleborine*. In the eastern part of the native range, the suitable habitats are also located in eastern coast of the Black Sea, the south-western Himalayan foothills, North and South Korea and Japan. Some available niches are also found along the Aleutian Islands to Kodiak Island and Seward. In the invasive range, the model selected the western coast of North America from south-eastern Canada and Newfoundland to South Carolina in the south, and the eastern lowland regions of the USA. The model based on location from the native range only differs from the combined one in the lack of potentially suitable habitats in Japan and the lower

suitability of the eastern Black Sea region within the natural range. There are no proper niches in the eastern part of North America in this model, however, the Aleutian Islands, Kodiak Island and Seward seem to be possibly available for *E. helleborine*. The analysis also indicated the foothills of the Coast Mountains as an area of appropriate climatic parameters for the occurrence of the studied species. The last model, created using exclusively invasive locations indicated solely the central-eastern North America as a region where *E. helleborine* could grow in its invasive range. The visual differences between the models were confirmed in the range overlap test (I=0.3994, D=0.1847, RR= 0.7159). Moreover, the distribution of invasive and native populations is associated with different climatic factors. While the American range is related to the precipitation in the driest and coldest time of the year, the temperature limits the occurrence of Asian populations. The calculated niche similarity indexes were relatively high: I=0.897, D=0.685, RR=0.860. The future climatic changes will not affect fundamentally the geographical range of *E. helleborine*. The most significant modification of the distribution of its suitable niches are related to the A1b scenario. In all three analysed models the decrease of the total area of its habitats is observed. Potential loss range from 25% (A1b) to 40% (B2a).

The research results indicated the unique nature of the invasion of *E. helleborine*. While in the west coast of North America, the species occupied habitats very similar to the native Eurasian populations, the expansion in the east coast was related to niche shift. Because previous molecular studies did not indicate significant genetic differences between native and invasive populations of *E. helleborine*, the niche shift of east coast populations was probably not related to their genetic differentiation and it may be hypothesised that the adaptation was a result of the wide ecological amplitude of the species. While in its native range *E. helleborine* probably do not use the whole variety of its potentially available habitats, the orchid was forced to occupy areas characterized by different climatic conditions during invasion in North America. The wide ecological amplitude of the species also explains its rapid expansion in the New World – the genetic modification related to the invasion would require much more time. It seems that the orchid is already naturalized in the major part of its invasive range, in both east and west North American coasts and it should not be classified as agricultural or an environmental weed. Its presence in the central USA states of Montana,



Colorado and New Mexico is most probably ephemeral, however, those populations should be controlled due to the high invasive potential of the studied species and the theoretical possibility of hybridization with the only North American native *Epipactis* species, *E. gigantea*. Because the significant future habitat loss related to climate changes will be observed also in the native range of *E. helleborine*, the conservation actions should be taken.

Another studies concerned African invasive representative of Orchidaceae - *Oeceoclades maculata* [H4]. This species is widespread in the Neotropics and is usually classified as invasive (eg. Cohen & Ackerman 2009). Origin of the species in the Neotropics remains unverified, however, it was possibly transported to South America as numerous other plants aboard slave trading ships in XVI century. The further goal of the conducted study was also to identify climatic factors limiting current distribution of *O. maculata* as well as to estimate the modifications of its geographical range related to the climate changes in the future.

The potential niche modeling was based on the species presence-only observations. As input data 19 climatic variables developed by Hijmans et al. (2005) were used together with the altitudinal data. To assess potential expansion of invasive populations of *O. maculata* in 2080, three different climate change scenarios (A1b, A2a and B2a) were applied into modeling. The datasets used in the analysis were developed by CGIAR Research Program (Ramirez & Jarvis 2008). ENMTools application was used to calculate the overlap of the future potential ranges of the orchid. To define the similarity of the niches occupied by *O. maculata* in various parts of its range three datasets were compiled – 1<sup>st</sup> one encompassed African records of the species, 2<sup>nd</sup> Neotropical data, and 3<sup>rd</sup> included all known locations. The niches similarity was calculated using Schoener's D and I statistics (Schoener 1968, Warren et al. 2008) implemented in ENMTools.

The analysis revealed significant differences in the ecological niches occupied by American and African populations of *O. maculata* (D=0.353, I=0.635). For both groups the temperature seasonality was the main factor limiting their distribution. While the Neotropical populations seem to be more sensitive to the annual temperature shifts, the occurrence of the African populations depends also on the rainfall. The models created for 2080 indicated

substantial differences in orchid potential range in various climate change scenarios, however, the modifications are observed mainly along the boundary of the currently occupied territory.

The study indicated that the current status of *O. maculata* as an invasive species should be reconsidered and possibly this orchid should be recognized as a naturalized plant in South America where the species has already occupied most of the available niches. However, in North America, there is a great possibility of further spread of this orchid into undisturbed natural areas, especially in Florida, and thus its status as an invasive plant should be maintained.

Another invasive representative of Orchidaceae reported from Neotropics is *Arundina graminifolia* (D. Don) Hochr. Unlike *O. maculata*, this Asian plant began its expansion in North America and the Caribbean in 60' of XX century. Currently the invasive range of *A. graminifolia* extends from USA south to Colombia and Peru. The aim of the conducted study [H5] was to define the niche conservatism of this species and to analyse its future invasive potential.

To estimate the similarity between habitats occupied by Asian and Neotropical populations of *A. graminifolia* the database of its localities was divided into two groups: invasive and native. Except Schoener's D and I statistics used in the previous study, the relative rank index (RR), Pearson's correlation coefficient (C, Warren & Seifert 2011) and bias metric were used. To visualize the differences between niches occupied by invasive and native populations, a principal component analysis (PCA) was performed. The future climatic projections related to a hypothetical climate change between 2020 and 2080 with scenarios A1b, A2a and B2a (Ramirez & Jarvis 2008) were used to estimate the future distribution of suitable habitats of *A. graminifolia*. The dynamics of the distribution of the niches were assessed within three areas: the whole world, Southeast Asia (native range of the species; 38°N–27°S, 60°E–176°W), and South America (current invasive range of the species; 35°N–60°S, 125° W–24°W).

The study indicated substantial niche conservatism of *A. graminifolia*. The invasion of this species in Neotropics was not related to the adaptation to the new habitat conditions. The analysis showed that invasive populations occupy only some of the niches that would be available for the native specimens. The PCA analysis indicated that the Neotropical locations

are placed within Asian ones forming a part of the native range. Within Asian range the distribution of studied orchid is limited mainly by rainfall, while the occurrence of Neotropical populations is related to the isothermality. The future climatic changes will not affect drastically the general geographical range of *A. graminifolia*, however, the coverage of the suitable niches will decrease in all three analysed scenarios. The significant reduction of the habitats was indicated in A1b and A2a models. Any future decrease in suitable niches as a result of climatic changes would be more significant in invasive range where the potential habitat loss may reach even 88%.

### ENM in historical biogeography studies

- Kolanowska M. 2013. Glacial refugia and migration routes of the Neotropical genus *Trizeuxis* (Orchidaceae). *Acta Soc. Bot. Pol.* 82(3): 225-230.
- Kolanowska M. 2014(2015). Determination of potential glacial refugia and possible migration routes of *Campylocentrum* (Vandaeae, Orchidaceae) species through the Darién Gap. *Acta Soc. Bot. Pol.* 84(1): 97-102.
- Kolanowska M., Szlachetko D. L. 2014. Niche conservatism of *Eulophia alta*, a trans-Atlantic orchid species. *Acta Soc. Bot. Pol.* 83(1): 51-57. (DOI: 10.5586/asbp.2014.007)
- Naczka A., Kolanowska M. 2015. Glacial refugia and future habitat coverage of selected *Dactylorhiza* representatives (Orchidaceae). *PLoS ONE* 10(11): e0143478.
- Kolanowska M., Mystkowska K., Kras M., Dudek M., Konowalik K. 2016. Evolution of the climatic tolerance and postglacial range changes of the most primitive orchids (Apostasioideae) within Sundaland, Wallacea and Sahul. *PeerJ* 4:e2384.

As mentioned in the introduction, classical paleontological analyses of past distribution and estimation of migration routes cannot be used in the studies on Orchidaceae due to the lack of fossil material.

The aim of the research was to estimate the distribution of the suitable habitats of the monospecific orchid genus *Trizeuxis* Lindl. during the last glacial maximum (LGM, ca. 26500-19000 years ago) and to determine its potential migration routes using ecological niche modeling (ENM) methods. The studied species is an epiphytic plant, most often growing on

*Psidium guajava* L., as well as representatives of *Citrus* L. and *Coffea* L. The close relation between *T. falcata* Lindl. with the phorophyte was used to identify the possible glacial refugia of this orchid.

The distribution model for LGM was created using the georeferenced locations of *T. falcata* and *P. guajava* populations as well as 19 climatic variables developed by Paleoclimate Modeling Intercomparison Project Phase II (Braconnot et al. 2007) and the digital elevation map. To estimate the location of the studied orchid refugia, the map of its potential glacial range was compiled with the analogical model designed for *P. guajava*. The combined map was therefore compared with the current range of *T. falcata* enabling the identification of potential directions of its post-glacial migration.

The other research concerned postglacial migration of *Campylocentrum* Benth. representatives through the Darién Gap which separates Panamanian province of Darién from Colombia [H7]. Also in this study the bioclimatic variables developed by Hijmans et al. (2005) and Braconnot et al. (2007) together with the digital elevation map were used. Four species, *C. brenesii* Schltr., *C. micranthum* (Lindl.) Rolfe, *C. panamense* Ames, and *C. tyrridion* Garay & Dunst., were included in the analyses. The database of the localities of these species was compiled based on revision of herbarium material and conducted field studies. The most probable refugial areas of *C. brenesii* included Sierra Madre de Chiapas, Cordillera de Talamanca and Cordillera de San Blas. Refugia of *C. micranthum* were located in Chiapas Highlands, Cordillera Chontaleña, Cordillera de Talamanca, Serranía de Tabasará, Cordillera de San Blas and Serranía del Darién in Mesoamerica, as well as in Colombian Serranía de Abibe, Serranía de San Jerónimo, Serranía de Ayapar. Region of Bocas del Toro, Panama Canal and Colombian Pacific Coast excluding Serranía del Baudó probably were refugial areas of *C. panamense*. The potential refugia of *C. tyrridion* were located in the coast of Gulf of Panama, Serranía Del Sapo, coasts of Gulf of Morrosquilo, Cartagena Bay, Maracaibo Lake as well as Ecuadorian coast of Bay of Sardinas. Based on the distribution of the possible refugia during the last glacial maximum and the present ranges of the studied *Campylocentrum* species, their migration routes through the Darién Gap were estimated. The results of analyses indicated also regression of potential range of *C. panamense*.

Techniques used in studies on *Trizeuxis* and *Campylocentrum* can be used in all research on distribution of glacial refugia and postglacial migration of other plants which remains are not observed in fossil material or for which the amount of this relics is insufficient for conducting classical palaeobotanical analyses.

Further studies [H6] concerned a trans-Atlantic species, *Eulophia alta* (L.) Fawc. & Rendle. This taxon is the sole representative of the genus in Neotropics. It occurs also in Africa, where the majority of *Eulophia* species is distributed. Except of analysis of distribution of glacial refugia of this species the research goal was to evaluate the degree of its bioclimatic niche conservatism.

The database of the studied orchid records was divided into two groups – African and Neotropical. For both sets, the ecological niche modeling for present time (Hijmans et al. 2005) and last glacial maximum (Braconnot et al. 2007) was conducted. Moreover, for both groups the limiting factors were calculated and the differences between their niches were evaluated (Schoener 1968, Warren et al. 2008).

As the result of conducted studies, the glacial refugia of *E. alta* were determined. Based on the paleovegetation reconstruction maps (Olson et al. 1983) those areas were covered during LGM with seasonal tropical forest as well as with tropical savanna and woodland. The distribution of the glacial suitable niches of *E. alta* corresponds to the current maps of potential range of this species. Yet, the differences between the currently occupied niches on both continents are significant ( $D=0.657$ ,  $I=0.883$ ). This fact, combined with the lack of significant morphological differences suggests preglacial separation of *E. alta* population and their independent adaptation to bioclimatic conditions. The most important climatic factor limiting distribution of the species in both the Old and the New World is temperature seasonality. In Americas the occurrence of *E. alta* is also related to the rainfall in the coldest quarter, while African populations are associated with the mean temperature of the coldest quarter.

As mentioned before, *E. alta* is the only representative of the genus considered as a natural element of Neotropical flora. However, it should be noted that in 2007 the expansion of Asian *E. graminea* Lindl. was reported in Florida. This species was previously listed as an invasive taxon in the territory of the Republic of South Africa and Australia. Currently the

low number of this orchid localities outside its native range prevent conducting a fully reliable biogeographic analysis, also due to the unknown naturalization status of the plants on each continent. Nevertheless, the gathered data enabled the comparison of ecological niches occupied by invasive and Asian populations. Preliminary study results were presented in BioDivEvo2014 conference which was held on 24-27 March 2014 in Desden (Kolanowska M. 2014. Niche conservatism and potential future expansion of *Eulophia graminea*. ss. 123-124. [In]: BioDivEvo2014. Senckenberg Naturhistorische Sammlungen Dresden). The conducted analysis indicated a substantial niche similarity between the two groups ( $I=0.898$ ,  $D=0.706$ ) despite the differences in the major factors limiting their distribution. According to obtained results, the future climate changes will not substantially affect the *E. graminea* range.

The development of molecular techniques allowed to conduct phylogeographical analyses which were used to investigate the past distribution of *Dactylorhiza* Neck. ex Nevski representatives (i.a. Nordström & Hedrén 2008, Ståhlberg & Hedrén 2008). The goal of my next study [H8] was to compare the information on localization of glacial refugia of *Dactylorhiza* species obtained in genetic research with the results of ENM analysis. Moreover, the impact of future climate changes on the habitats preferred by studied plants was evaluated as it was done in previously discussed papers [H1, H3, H4]. In this study representatives of *Dactylorhiza incarnata/maculata* complex were analysed using above mentioned methods.

The research confirmed the location of glacial refugia of *D. majalis* ssp. *traunsteineri* around the Alps. the suitable niches of *D. majalis* ssp. *lapponica* and *D. majalis* ssp. *majalis* were located further to the south in the ENM analysis (e.g. Corsica, the southern Apennines, the southern coast of the Sea of Azov). The study confirmed previously published hypothesis on the distribution of glacial refugia of *D. incarnata* s.l. (e.g. Hedrén 2001, Pillon et al. 2007) which were located in Corsica, the southern Apennines, the southern Balkans and the northeastern coast of the Black Sea. Unlike molecular studies, ENM analyses did not indicate central Europe or central Russia as climatically suitable during LGM for occurrence of *D. maculata* ssp. *fuchsii* or *D. maculata* ssp. *maculata*. Simulations of suitable habitats coverage

modification related to the climate changes showed significant decrease of preferred niched of studied species (except of *D. incarnata* var. *incarnata*).

This research indicated necessity of merging molecular studies with ENM analyses to achieve more precise estimation on the distribution of glacial refugia of Orchidaceae. Research on molecular patterns of geographical distribution of various genetic lineages within the species can be made only for taxa for which it is possible to collect a sufficient number of molecular data. The limitations in this kind of study will probably involve tropical orchids, for which no sufficient amount of samples is available, but certainly phylogeographical analyses can be used in the research on Eurasian and North American plants.

The further historical biogeographical research, which I conducted with collaborators, concerned phylogenetic niche conservatism [H9]. The analyses were made for the most primitive orchids – subfamily Apostasioideae. This taxon has been intensively studied before in the aspects of morphology, anatomy and genetic relationships, but no research on biogeography has been conducted. To evaluate distribution of glacial refugia 12 climatic variables were used and the study area was limited to 53°S–47.8°N, 88°–190°E. Except of ENM analysis, the phylogenetic research was conducted. Based on obtained phylograms and predicted niche occupancy profiles the evolution of climatic tolerance within Apostasioideae was reconstructed. The ENM analysis did not indicate any significant changes in the distribution of the suitable niches of most of the studied taxa. The niche conservatism of Apostasioideae is relatively high, and the tolerances of the studied climatic variables of the representatives of this group are rather narrow. The intensive diversification of climatic tolerance began ca. 21 Ma ago. Noteworthy, for the most of analysed variable no significant infrageneric niche conservatism was observed - in some cases representatives of *Apostasia* Blume shared more habitats with *Neuwiedia* Blume than with other congeners. The analogical studies should be conducted for other subfamilies recognized in Orchidaceae as they can be crucial for identification of the diversification reasons of various taxa.

### **ENM in taxonomic studies**

- Szlachetko D.L., Górniak M., Kolanowska M., Mytnik-Ejsmont J., Kowalkowska A., Rutkowski P., Koliński T. 2014. Taxonomic position and phylogeny of the genus

*Vargasiella* (Orchidaceae, Vandoideae) based on molecular and morphological evidence. PLoS ONE 9(6): e98472.

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Despite intensive morphological studies which were conducted since the beginning of XX century and development of phylogenetic analyses, classification of Orchidaceae and the generic diversity within numerous subtribes remain topics of serious discussion between taxonomists (e.g. Schlechter 1926, Garay 1972, Dressler 1993, van den Berg et al. 2005, Chase et al. 2015, Freudenstein & Chase 2015). The epiphytic habit, CAM photosynthesis, and pollination via Lepidoptera or euglossine bees were considered as factors triggering enormous specific diversity of Orchidaceae (Givnish et al. 2015). However, previously no attempts to include elements of historical biogeography in taxonomic research were undertaken despite the fact that geographical analyses could explain the separation of the multiple evolutionary lineages of Orchidaceae and subsequent speciation.

Previously described study of phylogenetic niche conservatism in Apostasioideae [H9] was the first step allowing to determine the effect of changes in the climatic tolerance on the evolution of Orchidaceae. I decided to include analysis of a relatively recent history, last glacial maximum, in the taxonomic research on Neotropical genus *Vargasiella* C. Schweinf. [H3]. The systematic position of this taxon which was described in 1952, for years remained a contentious issue. The ENM tools were used in these study to reconstruct location of glacial refugia of *Vargasiella* and closely related genera (*Warrea* Lindl. and *Warreopsis* Garay) as well as to estimate postglacial changes in the distribution of their preferred niches. 19 previously mentioned climatic variables developed by Hijmans et al. (2005) and Braconnot et al. (2007) together with the digital elevation map were used. Spatial overlap of preferred habitats of studied taxa was estimated using the aforementioned indexes (I and D). The analyses indicated the location of refugia of *Vargasiella* in the Central Andes. The calculations of the ranges and niches overlap between models for the studied time periods indicated not the current regression of *Vargasiella* range in response to warming climate after the LGM. The estimated suitable habitats for the occurrence of *Warrea* and *Warreopsis*



species during LGM were probably located in warmer lowland to lower montane regions of Mesoamerica and Northern South America and no significant changes in their geographic ranges or occupied niches are observed in the present time. This was the first comprehensive research on morphology, phylogeny and biogeography of *Vargasiella* and the only study that showed significant differences in post-glacial history between this taxon and its closest relatives.

I used ENM techniques also in taxonomic studies on *Psilochilus* Barb. Rodr. [H10]. Representatives of this taxon are small, terrestrial plants producing inconspicuous flowers. There are difficult to find during the field studies and due to this fact a small number of collections are deposited in herbaria. An inadequate amount of available research material limited possibility of conducting any analysis regarding their climatic tolerance. In my research I used ENM techniques to determine the degree of overlap of preferred climatic niches between morphologically similar *Psilochilus* species. The geographical range of most of the genus representatives is limited by isothermality and temperature seasonality. Taxa sharing similar vegetative architecture and/or flower structure occupy different bioclimatic niches. Analogical studies can be carried out for other poorly known genera for which availability of data on habitat requirements is limited. The ENM analyses would constitute a valuable clue in the research on taxa within which the presence of ecotypes is suspected.

## Summary

The studies discussed above were the first in the history of investigation on Orchidaceae research in which the ENM techniques were used. In a short time the results of my analyses have been used by other scientists, not only botanists (e.g. Beauséjour 2015, Matos Medina 2016, Wang et al. 2017). No other previous taxonomic studies on tropical orchids included historical analysis, which certainly is a valuable clue in the investigation of speciation within numerous groups of organisms.

One of the most important results of my research was proving the heterogeneous nature of the expansion of *E. helleborine* in North America. Previous studies indicated the tendency to retain the niche of the species in its non-native range (eg. Palaoro et al. 2013), other have proved a change in the occupied habitat in the invaded area (eg. Broennimann et

al. 2007). In the studies on *O. maculata* and *A. graminifolia* I used tools for modeling and analysis of bioclimatic niche in order to determine the current naturalization status of invasive species. In addition, these studies allowed to identify areas that are predisposed by the climatic conditions as potential zones for further expansion of studied taxa. A similar workflow can be successfully used to verify the status of other non-native organisms and to recognize areas that should be subject to long-term monitoring. It is worth to notice that the proposed scheme of analysis can be applied also in the studies on the ecological diversity of the populations of species characterized by a significant range disjunction. Since transatlantic disjunction is observed in about 110 angiosperms genera (Renner 2004), the technique of ecological niches modeling may be helpful in numerous botanical surveys.

The most promising elements of research, which certainly may be applied in many research on the evolution of different groups of organisms, include analysis of phylogenetic niche conservatism and the evolution of the climatic tolerance. As shown in the above-discussed studies on Apostasioideae ENM techniques combined with phylogenetic analyses can be used to determine the effect of bioclimatic tolerance conservatism on diversification among various taxa.

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## 5. OVERVIEW OF OTHER SCIENTIFIC ACCOMPLISHMENTS

### 5A. Prior to obtaining Ph.D. degree

I began to study Orchidaceae during master's studies by conducting research on the morphological and genetic variability of local populations of *Dactylorhiza incarnata* and leading investigation on the orchid flora of Pieniny National Park. Simultaneously, together with employees of the Department of Plant Taxonomy and Nature Conservation I have participated in the development of effective methods of metaplantation of threatened orchids (*Epipactis atrorubens*, *E. helleborine*).

In 2008 I was awarded in the contest entitled “Colombia – megadiverse country” organized by the Embassy of the Republic of Colombia in Poland (supported by the Ministry of Environment) and I had the opportunity to internship in the El Cocuy National Park in northern Colombia. This practicum was related to the "Guardaparques Voluntarios" program of Special Administrative Unit for the National Parks of the Ministry of Environment, Housing and Territorial Development of Colombia. This experience prompted me to choose Colombian Orchidaceae as a main study object during doctoral studies. The project entitled “Biodiversity of the Colombian department of Valle del Cauca - study of the family Orchidaceae“ received financial support of the Ministry of Science and Higher Education (project N N304 043939).

I had the opportunity to conduct studies in the leading scientific institutions, including Harvard University, the Missouri Botanical Garden, Naturhistorisches Museum Wien, or the Royal Botanic Garden Kew. The collaboration with local scientists lead to publication of a bilingual (English-Spanish) monograph "Orchids of the Yotoco Forest Reserve, Colombia". Moreover, the teamwork resulted in the preparation of a series of papers published in peer-reviewed journals [i.e. A1, A2, B3, B7, B8]. Preliminary results of the studies on the orchid flora of the department of Valle del Cauca were presented in 2011, at the conference BioSystematics, which was held in Berlin.

On 18 May 2012 I successfully defended my Ph.D. thesis which has been distinguished by the Faculty of Biology and awarded by the Gdansk Scientific Society in the field of Earth sciences.

## 5B. After obtaining Ph.D. degree

After obtaining Ph.D. degree I continued my research on Neotropical Orchidaceae. Once the studies on orchid flora of the Colombian department of Valle del Cauca were finished I published a series of four monographs that included characteristics of all species occurring in this area, keys for their identification as well as distribution maps.

One of the most important taxonomic studies which I conducted were devoted to generic delimitation within *Erycina*-complex. Based on the molecular analysis of the subtribe Oncidiinae, scientists from University of Florida proposed to include representatives of *Psygmorchis* and *Stacyella* into *Erycina*. The aim of the conducted research was to evaluate the morphological differences between the taxa in question. Specimens deposited in nine European and American herbaria were examined. In the result of the comparative studies of both vegetative and floral characters of those plants it was proposed to keep all three taxa in the generic rank [A23]. Representatives of *Psygmorchis* are characterized by the lack pseudobulbs and fan-shaped arrangement of leaves, while *Stacyella* species can be distinguished from *Erycina* based on the presence of leaf sheaths at the base of pseudobulbs. Moreover, as a result of the revision of herbarium material two new species of *Psygmorchis* were described.

Another taxon which specific diversity required revision was the only Neotropical representative of Angrecinae – the genus *Campylocentrum* which was described in 1881. It includes both leafy and leafless plants producing non-resupinate, tiny flowers arranged into lateral, dense inflorescences. The tepals are free or partially fused and the spurred lip is entire or 3-lobed. Short gynostemium of those plants is slender or ornamented with small appendages on both sides of the stigma. The research revealed numerous mistakes in the previous determinations of the genus representatives that were probably caused by the identification of those orchids by the taxonomists based solely on their vegetative characters. The type specimens of *Campylocentrum* species deposited mainly in the European herbaria were examined in order to conduct comparative research and to ensure the correctness of further identifications. The studies resulted in description of 12 new *Campylocentrum* species. The majority of them was found in the Republic of Colombia [i.e. A24, A28]. Additionally,



the status of *Angraecum weigeltii* was revised. This orchid was previously considered as synonymic with *C. fasciola*, but the research indicated the significant differences in the structure of flowers (lip and spur) between both species. Therefore, a new combination within the genus, *Campylocentrum weigeltii*, was proposed [A14].

Thereafter, the study on the high-montane genus *Pterichis* was conducted. This taxon was described in 1840 and it includes terrestrial plants with basal leaves which are often absent during flowering. The non-resupinate flowers of *Pterichis* are arranged in the racemose inflorescence. Both the floral bracts and ovaries are densely ciliate or pubescent. The lip is concave, usually ornamented with numerous appendages along the margin. The gynostemium is short, lacking any appendages. The geographical range of *Pterichis* extends from Costa Rica south to Argentina, with the greatest species diversity in the Andes. Populations usually grow in high-montane shrubs or grassy paramo, but their occurrence was also reported from Andean forest above the altitude of 2600 m. The aim of the studies was to evaluate specific diversity of *Pterichis* in Colombia. For the first time the representative of the genus was found in this country in 1920 and in the most recent floristic list of Colombian orchids nine species of *Pterichis* were included. The study resulted in describing six new species of the genus [i.e. A8, A15, A51, A72, B22].

During the examination of herbarium material, the data for the study of orchid flora of the Republic of Colombia were gathered. While the extensive publications on Orchidaceae of the neighboring countries have been published years ago, the existing knowledge on the Colombian representatives of the family is limited to morphological descriptions of genera and the list of species which was published in 2007. Together with employees of the Department of Plant Taxonomy and Nature Conservation of the University of Gdansk and Colombian scientists I described over 50 new species representing more than 20 orchid genera [i.a. A3-A13, A15-A18, A29-A33, A40-A42, A49]. Also a complete revisions of several Colombian taxa, i.a. *Mesadenella* [B23], *Myrosmodes* [A46] oraz *Takulumena* [A53] were published. Moreover, the examination of herbarium material resulted in further discoveries of new species from other Neotropical countries, i.a. Ecuador [A48, A70], Costa Rica [A27] and Venezuela [A10, A17, A61].

Other floristic studies on Orchidaceae were concerned the Isthmus of Darién, one of the most poorly-known region of the world. As a result of conducted research several new species occurring in this area were described [A19, A47] and in 2014 a monograph that included information about all species reported from this region with the identification keys was published.

In 2013 the status of *Ponthieva micromystax* was revised. [A26]. This taxon has been never formally described and the mentioned name was written on two herbarium sheets deposited in the Naturhistorisches Museum Wien. All specimens were gathered by the same collector in the territory of the Republic of Colombia, but our studies revealed that these plants belong to two different genera. The first one is a representative of *Ponthieva*, however, it do not represent any described species of this taxon. The second sheet contains specimens of *Ocampoa* - the genus that was previously considered as monotypic Mexican taxon. Hereby, as a result of studies two new taxa were described - *Ponthieva micromystax* and *Ocampoa kraenzliniana*.

Further taxonomic studies were focused on Central American genus *Deiregyne*. The specific composition of this taxon is discussed by botanists since the 80s of the XX century. Discrepancy in the presented concepts was a result of lack of indication of the generitype for *Deiregyne* during the genus description. In 1982 two studies on spiranthoid orchids were presented, but their authors proposed altered lectotypes for *Deiregyne* - *Spiranthes chloraeiformis* and *S. hemichrea*. Further Spiranthinae classification systems differed in terms of the approved type and that led to the inconsistency in the generic delimitation within the subtribe and to disagreement on the specific composition of *Aulosepalum* and *Burnsbaloghia*. In the result of conducted study it was recommended to typify *Deiregyne* by *S. hemichrea*. The proposal was published in Taxon journal [A25].

The aim of another taxonomic research which I conducted was a revision of the genus *Psilochilus* which was described in 1882. Representatives of this taxon produce fleshy, villose roots that arise from the basal nodes of the rhizome. The plicate leaves of those plants are distributed along the erect stem. The resupinate, inconspicuous flowers of *Psilochilus* are arranged in a terminal raceme. The tepals are free and the clawed, 3-lobed lip is ornamented with one to three adaxial, longitudinal calli. The gynostemium is elongate, more or less

arcuate, slender in the lower half and slightly swollen at the apex. Species of *Psilochilus* are terrestrial plants and they usually grow in wet montane and cloud forest. Populations were found in the coastal areas at the altitudes of about 200 m, as well as in montane regions (up to about 2500 m). The geographical range of the genus extends from southern Mexico south to Brazil. Until 2012 the genus included only seven species, however, the conducted studies revealed the existence of several additional taxa [e.g. A9, A21, A22, A34, A61] and a complete synopsis of *Psilochilus* was published in 2016 [H10].

In 2014 the studies on classification and diversity of Oncidiinae were intensified. The taxonomic status of several taxa, which specific composition was modified in 2012 based on results of molecular studies, was revised – e.g. *Brevilongium* and *Otoglossum* [A38], *Heteranthodium* [A54], *Cyrtochilum* [A90], *Brassia* [A62], *Odontoglossum* [A68], *Cohniella* [A79], and *Trichocentrum* [A83]. Moreover, numerous new species of oncioid orchids were described, e.g. *Heteranthodium* [B41], *Caucaea* [B46], *Cyrtochilum* [A37, A52, A56], *Diadenium* [A70], *Neokoehleria* [A71]. One of the most important outcome of the conducted studies was discovery of new species of *Hirtzia* [A35] and presentation of a taxonomic revision of this genus [A59]. Research on Neotropical subtribe Pachyphyllinae resulted in publication of a comprehensive synopsis of this taxon, including characteristic of newly described genus *Valdiviesoa* [A38]. Furthermore, new species of the nominal genus, *Pachyphyllum* were discovered [A36, A42].

In 2016, based on the conducted field studies and herbarium material examination, identity of *Selenipedium chica*, the nominal species of *Selenipedium*, was revised. Over the years it was assumed that the only specimen of this species from the original collection was deposited in herbarium of Naturhistorisches Museum Wien (W) and that no flower was fully preserved. The examination of plants stored in Muséum National d'Histoire Naturelle (P) revealed that the well preserved floral part are in fact deposited in this herbarium. Verification of the actual morphological characteristic of type specimen of *S. chica* allowed to recognize subspecies within this taxon. Moreover, data gathered in herbaria of the Harvard University (AMES), Universidad Nacional de Colombia (COL), the Royal Botanic Gardens (K), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), Universidad de

Nariño (PSO), Río Palenque Science Center (RPSC), and the Naturalis Biodiversity Center (U) resulted in description of two additional species of *Selenipedium* [A75].

As my main achievements in the field of floristic and taxonomic research I consider studies on Orchidaceae of the Darién Gap and publication of series of papers dedicated to generic delimitation within subtribe Oncidiinae [e.g. A38, A54, A62, A68, A79, A83, A90]. The discovery of a new species of *Telipogon*, named *T. diabolicus* in reference to the form of gynostemium and lip callus [A80], during the field works conducted in southern Colombia attracted the attention of the national and international media (i.a. the Washington Post and National Geographic).

Currently I am working on cosmopolitan subtribe Habenariinae. The part of this study is collecting data that will allow to reconstruct evolution of bioclimatic tolerance within this taxon. Additionally, I am conducting analyses that will reveal the impact of future climatic changes on saprophytic orchids.

Kolanowska