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ORIGINS OF NATIVE VASCULAR PLANTS OF ANTARCTICA: COMMENTS FROM A HISTORICAL PHYTOGEOGRAPHY VIEWPOINT



*The article provides an overview of the problem of origin of the only native vascular plants of Antarctica, *Deschampsia antarctica* (Poaceae) and *Colobanthus quitensis* (Caryophyllaceae), from the viewpoint of modern historical phytogeography and related fields of science. Some authors suggested the Tertiary relict status of these plants in Antarctica, while others favour their recent Holocene immigration. Direct data (fossil or molecular genetic ones) for solving this controversy is still lacking. However, there is no convincing evidence supporting the Tertiary relict status of these plants in Antarctica. Most probably *D. antarctica* and *C. quitensis* migrated to Antarctica in the Holocene or Late Pleistocene (last interglacial?) through bird-aided long-distance dispersal. It should be critically tested by (1) appropriate methods of molecular phylogeography, (2) molecular clock methods, if feasible, (3) direct paleobotanical studies, (4) paleoclimatic reconstructions, and (5) comparison with cases of taxa with similar distribution/dispersal patterns. The problem of the origin of Antarctic vascular plants is a perfect model for integration of modern methods of molecular phylogeography and phylogenetics, population biology, paleobiology and paleogeography for solving a long-standing enigma of historical plant geography and evolution.*

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Introduction

This article was provoked by the article by I.Yu. Parnikoza, D.N. Maidaunuk, and I.A. Kozevetska [1] recently published in «Cytology and Genetics» (Kyiv). We cannot completely agree with one of the main conclusions of the authors, who postulated the Tertiary (Oligocene-Pliocene) relict status for both angiosperm taxa in Antarctica, and because of that we provide here some additional information and comments on the topics considered in the article by Parnikoza et al.

Due to the tremendous progress in and growing availability of molecular methods, the science of historical biogeography is now undergoing rapid and dramatic transformation which can be regarded as a true «molecular revolution» [2–9]. In fact, instead of vague and non-testable hypotheses and assumptions, we have now in many cases a solid evidence indicating possible centers of origin, migration pathways and timing of evolutionary radiations for many previously enigmatic biogeographical cases concerning many taxa of plants, animals, fungi, and even protists. It means that we see the transformation of a previously empirical field of science into a combination of real experimental and historical science, conclusions of which are falsifiable in the true scientific, Popperian sense. Molecular phylogeographic, phylogenetic, and populational-genetic approaches proved to be the most productive ones in reconstructing the history and development of geographical patterns in plants.

The most interesting examples bearing conceptual implications to our topic are, in our opinion, recent results obtained in biogeography in the fields of studying of classical vicariance and/or dispersal models, island biogeography (especially cases of dispersal to and evolution on oceanic islands), nothal biogeographical links (especially various explanations of nothal disjunctions), Late Pleistocene and Holocene history of the Arctic and boreal biota (especially studies using combined methods of phylogeography and paleobiology), and some others, which we cannot discuss here in detail because of space and time limitations.

Of course, it is impossible to cover sufficiently in the present article the vast scientific areas mentioned above. However, we will provide here some general ideas, striking examples, references to several most important and useful review articles, and, finally, our comments regarding the current concepts of the origins of Antarctic vascular plants, including the interesting concept proposed by

Parnikoza et al. [1]. Our brief review is by necessity a broad-stroke picture in which we cannot go into too much detail of the discussed extensive issues. However, we believe that interested readers will consult the references we cite here and get a wider and deeper vision of the important biogeographical and evolutionary problems, which are being successfully solved with the aid of methods of molecular ecology, phylogeography, population genetics, and other modern approaches.

Results and discussion

Dispersal and vicariance models in phylogeography. First of all, it should be emphasized that modern historical biogeography is, by definition, a historical and evolutionary science [3, 5]. It means that reconstruction of historical traits in dispersal and distribution of organisms is impossible without taking into consideration the evolutionary processes occurring in space and time. Non-evolutionary historical biogeography is thus a conceptual nonsense.

Vicariance models imply gradual migrations from the centers of origin and further changes of ancestral ranges, with their subsequent splitting in most cases of disjunction. Classical examples of vicariance models are explanations of present-day distribution patterns by past continental movements (mobilism, or modern plate tectonics), orogenesis, transgressions and regressions of seas, shifts of physiographic, climatic and biotic zones, etc.

On the other hand, dispersal models imply gradual or geologically momentary dispersal events, during which organisms or their dispersal units migrate over some physical barriers and become successfully established in a new territory, and such migrations are naturally accompanied and followed by evolutionary transformations.

Vicariance-based models were especially fashionable after the triumph of the Wegenerian mobilistic theory and further development of the modern theory of global plate tectonics. However, vicariance was also a respected concept even long before that. If we consider enigmatic distribution patterns of many plants in the Southern Hemisphere, this concept can be traced back to works of J.D. Hooker. In more detail these models and explanations are discussed in several review articles [4, 5, 10–14] and references therein, which are recommended to the reader for further acquaintance with the problem.

However, recently the vicariance models, especially those appealing and referring to Gondwanan biotic interactions, fell out of fashion for several reasons, which will be briefly discussed below using several case topics.

Insular endemics and long-distance dispersal. A flow of recent molecular phylogenetic and phylogeographic studies of insular floras and faunas indicated in many cases long-distance migration pathways and showed that suggestions of the relict status and ancient age of many oceanic endemics are often far from being justified [2, 15–20]. It is especially true for remote oceanic islands and archipelagos that have never been part of any continent and, consequently, are not suitable for vicariance biogeographical models.

The Hawaii is probably the best studied archipelago in that respect [21–25]. Some evolutionary links of endemic Hawaiian plants explained by long-distance dispersal are truly amazing. For example, the endemic Hawaiian woody species of violets (*Viola* sect. *Nosphinium*, family Violaceae) which were considered evolutionary «primitive» in fact evolved quite recently (probably in the Middle Pliocene) from the subarctic amphi-Beringian ancestors probably related to the modern herbaceous species of the polyploid *V. langsdorffii* Ledeb. aggregate through a long-distance dispersal by birds from Alaska or East Siberia and subsequent explosive radiation [21]. We can mention also the African links of Hawaiian *Hesperomannia* A. Gray (Asteraceae) [23] and the origin of a morphologically diverse group of several Hawaiian endemic genera of Lamiaceae (*Haplostachys* Hillebr., *Phyllostegia* Benth. and *Stenogyne* Benth.) from North American taxa of *Stachys* L. *sensu lato* [24]. Other striking examples indicating North American, South Pacific, African and Asian sources of recent colonization of the Hawaii are extensively discussed in recent literature [17, 22, 25].

It is especially important to stress that the Hawaiian Islands are in fact a volcanic «conveyor belt» in the Pacific, with a chain of volcanic islands emerging as the crust plates move over the magmatic «hot spots» in the mantle [22]. It means that the islands themselves are comparatively young, and they are arranged linearly according to their age, from the oldest northwestern islands (e.g., Kauai) having ca. 5.1 million years of history to the youngest southeastern islands (like the island

of Hawaii itself) just ca. 430 thousand years old [22, 25]. Yet this geologically young archipelago houses a tremendous biotic diversity, with many unique endemic taxa of high taxonomic ranks that evolved during just a few millions of years. It is commonly agreed that the Hawaiian biota is in fact a long-distance dispersal biota [16, 25].

In respect to the problem of the initial arrival of *D. antarctica* and *C. quitensis* to Antarctica, the examples of oceanic island biotas and colonization of such islands from migration sources located thousands of kilometers away show us that the Drake Passage (ca. 900 km) cannot be regarded as an ultimate barrier for eventual long-distance migrations from southern South America to Maritime Antarctica, even considering such additional obstacles as the Antarctic Polar Front and the Antarctic Circumpolar Current. Of course, the physical obstacles to migration of plants across the Drake Passage probably limited considerably the number of species that actually performed such random migrations. Another problem for migrants is to take a foothold in the new area and successfully colonize the inhospitable Antarctic shores, which was possible only to hardy plants preadapted to harsh environmental conditions. Thus, probably much more species in fact migrated from time to time across the Drake Passage, but only two species happened to be preadapted to the new conditions, which partly explains the scarcity of the Antarctic angiosperm flora.

Nothal floristic links: a legacy of Gondwana, migrations from the north, or long-distant dispersal phenomena? Recent studies convincingly demonstrated that many presumably Gondwanan groups in fact attained their present distribution through Laurasian migrations or/and long-distance dispersal [11–14]. Even *Nothofagus*, the long-cherished icon of adepts of nothal vicariance models [26, 27], probably experienced long-distance dispersal events in the course of its evolution [28]. However, it does not mean that all Gondwana-based historical-biogeographical explanations should be rejected. In fact, the Nothal biota of the Southern Hemisphere shows a complicated mix of different biogeographical models and patterns: there we can find examples of the real legacy of Gondwana (but only in some ancient enough groups!), southward migrations from the north (so-called boreotropical migrations), and numerous cases of transoceanic

long-distant dispersal phenomena [11, 14, 15, 29]. For further discussion see also reviews by Eskov in Russian [12, 13] and Mosyakin in Ukrainian [5] and references therein.

The changing views on the history (or histories) of the Nothal floras were reflected also in the recent proposal to modify the system of Takhtajan's floral kingdoms [30]. In particular, Cox [31] proposed to abandon the Antarctic Floral Kingdom and allocate its constituent parts to the neighboring kingdoms. Cox justly indicated that «The Antarctic floral Kingdom contains some (but not all) of the remains of a once-continuous southern Gondwana cool-temperate flora, now scattered into a relict distribution by the processes of plate tectonics, and present only where the persistence of cool, moist climates has allowed it to survive» [31]. We can add to that that some phytogeographic similarities of various parts of the Antarctic Kingdom are caused not only by plate tectonics events, but also, considerably, by long-distance dispersal events. Consequently, the Chile-Patagonian Region should be allocated to the Neotropical Kingdom. The Fernandezian Region and the Region of the South Subantarctic islands should be also placed there because of their long-distance dispersal links to the Neotropis. New Zealand and its surrounding islands should be transferred to the Australian Kingdom.

Thus, appeals of Parnikoza et al. [1] to publications emphasizing the high past biodiversity of Gondwana and its fragments in the Cretaceous and the Cenozoic has little or no implication to the question when and how modern *Deschampsia* and *Colobanthus* migrated to Antarctica. We know that Antarctica in the distant past was a much hospitable place than it is now; probably the great southern continent was the scene of evolution and migration of many important taxa now constituting the Nothal biota [29, 32–34], but interpretations of these data from the viewpoint of the modern biotic situation should be done carefully. It should be also evident that a find of a presumably caryophyllaceous flower *Caryophylloflora paleogenica* G. J. Jord. & Macphail in the Middle to Upper Eocene of Tasmania [35], mentioned by Parnikoza et al. [1], has nothing to do with the present-day distribution of *Colobanthus* (Caryophyllaceae) in Antarctica. Moreover, the taxonomic placement of that Eocene fossil in the family Caryophyllaceae *sensu stricto* is

tentative; probably this ancient plant belonged to some group of caryophyllids in a wider sense.

Late Pleistocene and Holocene history of the Arctic and boreal biota. Arctic, subarctic and Alpine plants are favorite models used in numerous molecular phylogeography studies, especially in Europe. Reviews of these studies from the viewpoint of the problem of Pleistocene relicts and refugia and Holocene floral migration routes have been recently published in Ukrainian [6, 7]; many other recent review publications are useful for a better vision of the Late Pleistocene and Holocene history of the Arctic and boreal biota [4, 8, 9, 36–40].

Moreover, it has been shown that, contrary to simplistic views of exclusively gradual «step-by-step» dispersal of most plants [41], the real Late Pleistocene – Early Holocene recolonization of glacial and periglacial areas of Eurasia and North America by plants developed mostly according to the long-distance dispersal scenario [15]. At the same time, hundreds of molecular phylogeography studies and state-of-the-art paleobotanical investigations showed that the concept of the «glacial steamroller» (or, better to say in this case, an «ice-roller»?) that exterminated nearly all life in glaciated and adjacent areas is also probably an exaggeration. Thus, «*tabula rasa*» and «*survival in situ*» models are not mutually excluding; both these explanations work for some taxa and specific areas, depending on many factors [4, 6, 7, 9, 37, 38, 40, 42]. No surprise—life is much more diverse than our mental models of it.

By analogy, comparing the available biogeographic cases of Arctic and Antarctic vascular plants, we can assume that (1) survival of *Deschampsia* and *Colobanthus* in Antarctica *in situ* since pre-Pleistocene times has a very low probability, (2) their Holocene migration (or probably even several migration events) to Antarctica is the most feasible explanation, and (3) their survival *in situ* during the Last Glacial Maximum (LGM) since one of interglacials is less probable, but not excluded.

Origins of native vascular plants of Antarctica: still in the mist. Here we will try to show some faults in discussion of Parnikoza et al. [1] when they attempt to prove the relict status of *D. antarctica* and *C. quitensis* in Antarctica and to pinpoint the age of their migrations. According to Parnikoza et al. [1], *D. antarctica* and *C. quitensis* migrated to Antarctica «during the Oligocene-Pliocene», when

the southern continent was less isolated and its climate was more favorable for naturalization of these taxa. Probably it was indeed less isolated and more favorable, but how is it related to the actual time of immigration of the two species in question? In the Cretaceous Antarctica was even less isolated from other Gondwana fragments and climatically more favorable than it was in the Oligocene-Pliocene and, judging from molecular-clock-based and fossil-calibrated age estimates, orders Caryophyllales and Poales, and probably even phylogenetically basal representatives of the families Caryophyllaceae and Poaceae, have differentiated already in the Late Cretaceous [10, 43, 44]. Should we because of that assume that *Colobanthus* and *Deschampsia* migrated to Antarctica already in the Late Cretaceous? Or probably in the Paleocene? Is there anybody voting for the Eocene? In the Oligocene palms were growing in Ukraine, but it does not necessarily mean that palms currently grown in Crimea are relicts and direct descendants of those Ukrainian Oligocene palms.

Sometimes researchers (usually except geologists and paleontologists) have problems with feeling the vastness of the geological timescale. It is simply nonsensical, from geological and paleobiological viewpoints, to guess as a migration age the age limit covering about 32 million years, or roughly a half of the whole Cenozoic [1]. The Early Oligocene started ca. 34 million years ago (Mya), while the Pliocene-Pleistocene boundary is currently placed at ca. 1.8 Mya [45].

Moreover, it is hard (in fact, impossible) to believe that Antarctic populations of both species, *D. antarctica* and *C. quitensis*, remained unchanged since the Oligocene, Miocene, or even Pliocene, and developed no visible morphological or considerable genetic distinctions from their relatives on the South American continent. That notion simply denies evolution, adaptive or neutral.

Parnikoza et al. [1] properly cited the results of Holderegger et al. [46], who found that Antarctic populations of *D. antarctica* show low genetic diversity. That fact may have several explanations, including the following most obvious ones: (1) Antarctic *D. antarctica* and *C. quitensis* are recent migrants that originated from limited founder stocks; the descendants of the founding populations simply had no time for genetic differentiation in Antarctica (the most parsimonious explanation,

by the way); and (2) there is a constant gene flow and/or migrations between the isolated Antarctic island populations of *D. antarctica* and *C. quitensis*, mixing their gene pools to the level of «low genetic diversity» [46]. If these species are capable of self-pollination and/or asexual reproduction (and they are!), then the assumption of their long-term isolation in combination with a genetic «melting pot» simply loses ground.

Let us consider just two examples: *Chenopodium tomentosum* Thouars (Chenopodiaceae) [47] and *Rumex frutescens* Thouars (Polygonaceae) [48, 49], both endemic to remote South Atlantic islands of the Tristan da Cunha (Tristan d'Acugna) group (ca. 2800 km from Africa and ca. 3200 km from the South American mainland), both evidently resulted from recent and single long-distance dispersal events, both having very close relatives in South America (taxa of the *Chenopodium ambrosioides* L. aggregate in the first case, and *Rumex cuneifolius* Campderb and other representatives of the predominantly South American subsection *Cuneifolii* Rechinger f. in the second), but still differing from them to the species or at least subspecies level. Why Antarctic plants do not differ, specifically or at least subspecifically or varietally, from their South American conspecific relatives, if they parted several million years ago?

Chwedorzewska [50], basing on AFLP analysis, reported that genetic diversity within the Antarctic populations of *D. antarctica* was greater than respective genetic diversity values within the analyzed Arctic populations of *D. brevifolia* R. Br. and *D. alpina* (L.) Roem. & Schult. sampled in Svalbard (Spitsbergen). Moreover, southern populations of *D. antarctica* revealed less diversity than northern populations living in less harsh conditions. These preliminary data can be interpreted in several ways. As we have seen from other examples (see above), low genetic diversity values within a species in a particular area may indicate a recent arrival of the species to that area and the founder effect. On the other hand, in the case of *D. antarctica* even a high genetic diversity can be interpreted as either (1) *in situ* genetic differentiation in isolated fragmented habitats and gradual but limited dispersal «by step-stones» or (2) a result of several independent long-distance migration events. There is also another option involving a bottleneck effect, when large portions of a population were eliminat-

ed due to high selective pressure of environmental conditions and/or random non-selective catastrophic events, such as advance of glaciers, sea level oscillations, and extreme climatic episodes. A reliable answer favoring any of these options can be obtained only through phylogenetic and phylogeographic studies involving wide-scale sampling of the species from all (or most of) known range fragments in Antarctica and many representative samples from South America.

Recent ITS analysis of *C. quitensis* demonstrated a relatively high genetic similarity among the studied Andean and Antarctic populations (sequence divergence = 1.17 %) despite the considerable geographical distance (> 3300 km) [51]. It should be also noted that *C. quitensis* is a selfing species, which is also capable of asexual reproduction. Of course, there was considerable ecotypic differentiation revealed, which should be expected in plants inhabiting so extreme and geographically isolated habitats differing considerably in local ecological conditions. Gianoli et al. [51] quite logically assume Andean origin of Antarctic populations of *Colobanthus* and its recent dispersal by migratory birds. Of course, we agree with Parnikoza et al. [1] that the ITS region sequences are probably not good markers of recent microevolutionary changes in *Colobanthus*, and other methods should be applied instead of or in addition to ITS phylogeny. However, before obtaining new data it would be safer to stick to the most parsimonious explanations.

If, as we have seen above, less than 5 million years was enough time in the Hawaii for evolution of endemic genera and spectacular evolutionary radiation of diverse species groups having in many cases just one recent ancestor per group that arrived by long-distance dispersal, if very recent migrants from South America to the islands of Tristan da Cunha were able to form distinct species differing from their South American relatives, then why, if we assume the «Oligocene-Pliocene» migration of *Deschampsia* and *Colobanthus* to Antarctica, these Antarctic plants developed no distinctions from their South American ancestors? Of course, one may say that tropical islands are probably more stimulating for evolutionary changes than the harsh Antarctic environment is. However, numerous examples demonstrate that in fact an escape from biotic competition enables dramatic island radiations, while abiotic environmental

stress is the leading factor promoting such radiations. Consequently, the amazing evolutionary conservatism indirectly implied by the assumption of the «Oligocene-Pliocene» origin of the two Antarctic species is simply inexplicable.

A recent molecular study of phylogenetic relationships of *Deschampsia antarctica* using ITS shed little light to the problem. In the trees obtained by Fernández Souto et al. [52] *D. antarctica* was grouped with five other *Deschampsia* species, but showed out in three different positions: (1) as a clade sister to all other *Deschampsia* species (excluding *D. flexuosa* (L.) Trin.), (2) as a sister group of *D. cespitosa* (L.) P. Beauv. – *D. alpina* (L.) Roem. & Schult. – *D. sukatschewii* (Popl.) Roshev., and (3) as sister to *D. mejlandii* C.E. Hubb. – *D. christopherseii* C.E. Hubb. In plain English it just means that the authors failed to pinpoint the phylogenetic position of *D. antarctica*, probably because of limitations of the methods or sequences used, or because of inadequate taxon sampling. Fernández Souto et al. [52] seem to be surprised by the revealed fact that «*Deschampsia* does not appear monophyletic as *D. flexuosa* is not included in this clade». It probably escaped their attention that *D. flexuosa* has been since long ago considered genetically distinct from *Deschampsia* s. str. and transferred into segregate genera, either *Lerchenfeldia* Schur (as *L. flexuosa* (L.) Schur) or *Avenella* Parl. (as *A. flexuosa* (L.) Drejer), and is currently treated taxonomically as a member of *Avenella*. This little example shows that some experience in traditional taxonomy is not unneeded even for molecular taxonomic studies.

Fascinating finds of a rich (of course, rich by Antarctic standards) fossil Neogene flora of the Meyer Desert Formation (the biostratigraphic age less than 3.8 Ma, which means an Early Pliocene or more recent age) in the Transantarctic Mountains prove that continental Antarctic in the Late Neogene was more suitable for terrestrial life than most people expected [32]. However, this fact has no bearing to proving the relict status of *Colobanthus* and *Deschampsia* in their present Antarctic ranges, as well as presence of broadleaf trees in boreal areas of Europe during interglacials does not necessarily mean that these trees survived *in situ* during glacial phases until the present day.

Glacial and climatic history of Antarctica should be also considered in detail before making any sug-

gestions on refugia of Antarctic vascular plants. Large-scale deglaciation in Antarctic coastal areas started with a general warming trend after 8.4 ka (thousand years ago). Before that many now ice-free Antarctic areas were glaciated [53–57]. It is evident from a multitude of sources that the global climatic history of the Late Pleistocene and Early Holocene was rather complex. The warming trend of the last deglaciation was interrupted by the Younger Dryas event that lasted for almost 1200 years (12.7–11.5 ka) and resulted in a reverse to almost glacial conditions. A short cold event occurred also around 8 ka.

For example, the deglaciation on South Georgia commenced prior to 18.6 ka; colder conditions returned after 14 ka and lasted during the Younger Dryas (12.7–11.5 ka) without significant changes, while the transition to postglacial conditions occurred between 8.4 and 6.5 ka and was interrupted by a cold event that began ca. 7.8 ka and lasted for ca. 400 years [58]. It is highly improbable that *Deschampsia* and *Colobanthus* survived such dramatic events *in situ* without any response, e.g. reductions of their ranges.

We should also not forget about eustatic sea level changes that reshaped and remodelled the coastal Antarctic areas and their biotas [59] and, consequently, influenced the potential and actual habitats of *Deschampsia* and *Colobanthus*; that makes their preservation *in situ* during diverse and dramatic Pleistocene events even more improbable.

However, a suggestion of survival of *D. antarctica* and/or *C. quitensis* during the LGM is no heresy. It might well be the case that these two angiosperms indeed survived the LGM in Antarctic islands, but it should be proved. In fact, the present climatic situation in Antarctica is rather unusual as compared to most periods of the Pleistocene, corresponding roughly to interglacial conditions [53, 57], especially if compared to the Last Glacial Maximum, both in the Northern [60] and Southern [55, 59] hemispheres. Some range expansions of several Antarctic species southward were observed recently; it is usually viewed as a response to global warming, although other causes, like normal climatic oscillations, should be also considered. Anyway, the present-day climatic conditions in Antarctica are much more favorable to plants than conditions there during the Last Glacial Maximum or other glacial maxima of the Pleistocene. Please

note that *D. antarctica* and *C. quitensis* (the first species being more widespread than the second) occupy now only a comparatively narrow northern strip of Maritime Antarctica, and these plants are already living virtually on the brink of survival. These considerations make the ideas of *in situ* survival of *D. antarctica* and *C. quitensis* in Antarctica since the Paleogene or even since the Early Pleistocene rather problematic.

Endemism and distribution patterns of various groups of plants and fungi (including lichens) occurring in Antarctica indicate that the Pleistocene survival was possible for some lichens, less probable for mosses [61], and rather improbable for the two considered species of vascular plants [see discussion in 62]. That was already evident to biogeographers of the first half of the 20th century. For example, consider discussions in the classical books by Wulff [63, 64], who often favored vicariance-based mobilistic historical explanations of plant distribution patterns, but did not extend such explanations to the two extant native species of Antarctic angiosperms. The reasons of the scarcity of the vascular flora of Antarctica should be also reconsidered from the viewpoint of both ecological and migrational factors. As Aleksandrova [65] correctly noted, the presence of just two species of flowering plants in Antarctica cannot be explained by extreme ecological factors only, because the ecological conditions for plants there are not worse than, for example, on the Franz Josef Land in the Russian Arctic. Consequently, we should consider such additional explanations as migrational obstacles and isolation of the region.

Indeed, solid evidence would be definitely needed for supporting the idea of the pre-Pleistocene age of *Colobanthus* and *Deschampsia* in Antarctica, but, as we see, no such evidence is available yet, while the bulk of both direct and indirect available data discussed in the present article speak in favor of the Holocene or, at best, Late Pleistocene age of the present-day Antarctic flowering plants.

Conclusions

The suggestion of Parnikoza et al. [1] of an Oligocene-Pliocene origin of *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. is most probably a gross overestimation. No data in their article, either literature or original, give convincing evidence supporting their concept of the

Tertiary age and relict status of these plants in Antarctica. It might have been better to critically assess an ample set of available evidence from classical historical biogeography, phylogeography, paleobotany, paleoclimatology and some other fields, not necessarily data regarding the two taxa and the territory considered, but also (and mainly) comparative data regarding other taxa and other areas with similar phytogeographical traits.

Judging from both direct and indirect evidence and comparison with biogeographical analogues, the most reasonable and consistent with facts suggestion would be that of the Holocene or Late Pleistocene (last interglacial?) age of migration of the ancestral stock of *D. antarctica* and *C. quitensis* to Antarctica through bird-aided long-distance dispersal events. Thus, these species (or one of them) are either Holocene migrants or, at best, relicts of a recent interglacial. In the last case they probably survived the Last Glacial Maximum (LGM) in coastal refugia in Maritime Antarctica or adjacent islands. However, these age estimations should be critically tested by (1) appropriate methods of molecular phylogeography involving extensively sampled plants from Antarctica and South America, (2) molecular clock methods, if feasible, (3) direct paleobotanical (including paleopalynological) studies, (4) paleoclimatic reconstructions, and (5) comparison with similar cases documented for taxa with similar distribution/dispersal patterns. Only in these directions lies the positive and reliable answer to the long-intriguing question of the origins of *D. antarctica* and *C. quitensis* in Antarctica.

The problem of the origin of Antarctic vascular plants is a perfect model for integration of modern methods of molecular phylogeography and phylogenetics, population biology, paleobiology and paleogeography for solving the long-standing enigma of historical phytogeography.

РЕЗЮМЕ. Дан обзор проблемы происхождения аборигенных сосудистых растений Антарктики *Deschampsia antarctica* (Poaceae) и *Colobanthus quitensis* (Caryophyllaceae) с точки зрения исторической фитогеографии и родственных направлений науки. Некоторые авторы считают, что эти растения в Антарктике являются реликтами третичных времен, а другие исследователи склоняются к концепции их недавней голоценовой миграции. Прямых данных (как ископаемых, так и молекулярно-генетических) для решения этой проблемы пока что не хватает. Тем не менее, нет

убедительного подтверждения третичного реликтового статуса этих растений в Антарктике. Вероятнее всего, *D. antarctica* и *C. quitensis* мигрировали в Антарктику в голоцене или позднем плейстоцене путем расселения на дальние расстояния с помощью птиц. Эта концепция должна быть критически проверена с помощью соответствующих методов молекулярной филогеографии, методов молекулярных часов (при возможности), непосредственных палеоботанических исследований, палеоклиматических реконструкций и сравнения с таксонами, имеющими аналогичные особенности распространения или расселения. Проблема происхождения антарктических сосудистых растений является замечательной моделью для интеграции современных методов молекулярной филогеографии и филогенетики, популяционной биологии, палеобиологии и палеогеографии для решения давней загадки исторической географии и эволюции растений.

РЕЗЮМЕ. Подается обзор проблемы происхождения единичных аборигенных судинных растений Антарктики *Deschampsia antarctica* (Poaceae) та *Colobanthus quitensis* (Caryophyllaceae) з точки зору історичної фітогеографії та споріднених напрямків науки. Деякі автори вважають, що ці рослини в Антарктиці є реліктами третинних часів, а інші дослідники схилиються до концепції їх недавньої голоценової міграції. Прямих даних (як викопних, так і молекулярно-генетичних) для вирішення цієї проблеми поки що не вистачає. Проте, третинний реліктовий статус цих рослин в Антарктиці не має переконливого підтвердження. Цілком імовірно, що *D. antarctica* та *C. quitensis* мігрували до Антарктики у голоцені або пізньому плейстоцені завдяки розселенню на далекі відстані за допомогою птахів. Ця концепція має бути критично перевірена за допомогою відповідних методів молекулярної фітогеографії, методів молекулярного годинника (при можливості), безпосередніх палеоботаничних досліджень, палеокліматичних реконструкцій та порівняння з таксонами, які мають аналогічні особливості поширення або розселення. Проблема походження антарктичних судинних рослин є чудовою моделлю для інтеграції сучасних методів молекулярної фітогеографії та філогенетики, популяційної біології, палеобіології та палеогеографії для вирішення давньої загадки історичної географії та еволюції рослин.

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