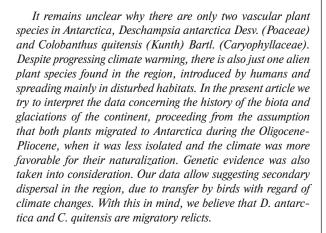I.YU. PARNIKOZA[1], D.N. MAIDANUK[2], I.A. KOZERETSKA[1]

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ARE *DESCHAMPSIA ANTARCTICA* DESV. AND *COLOBANTHUS QUITENSIS* (KUNTH) BARTL. MIGRATORY RELICTS?

It remains unclear why there are only two vascular plant species in Antarctica, Deschampsia antarctica Desv. (Poaceae) and Colobanthus quitensis (Kunth) Bartl. (Caryophyllaceae). Despite progressing climate warming, there is also just one alien plant species found in the region, introduced by humans and spreading mainly in disturbed habitats. In the present article we try to interpret the data concerning the history of the biota and glaciations of the continent, proceeding from the assumption that both plants migrated to Antarctica during the Oligocene-Pliocene, when it was less isolated and the climate was more favorable for their naturalization. Genetic evidence was also taken into consideration. Our data allow suggesting secondary dispersal in the region, due to transfer by birds with regard of climate changes. With this in mind, we believe that D. antarctica and C. quitensis are migratory relicts.

Introduction

The present-day flora of Maritime Antarctic includes only two species of vascular plants: *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae), both species found also in Subantarctic, Maritime Antarctic including the west coast of the Antarctic Peninsula southward to Alexander Island, and the Scotia Arc South Shetland, South Orkney and South Sandwich archipelagos. Here both species occur along the west coast of the Antarctic Peninsula south to the current southernmost site on Alamode Island, Terra-Firma Islands at 68° 42' S. On the eastern side of the Peninsula, adjoining the frozen Weddell Sea, vascular plants extend only as far south as 65° [1, 2]. These plants also occur in South America: *C. quitensis* extends along the Andes and one site in Mexico, and *D. antarctica* reaches central Chile neighbouring Argentina [3]. There are much more species of vascular plants in subantarctic areas; for example, the flora of the Kerguelen Archipelago numbers 36 to 69 species (data differ), and that of Tierra del Fuego reaches several hundred taxa [4—6]. *D. antarctica* and *C. quitensis* are thought to spread over Maritime Antarctic in the mid-Holocene [6—8]. But then, if one regards climate warming on the west coast of the Antarctic Peninsula during the last fifty years, it is difficult to explain the absence of other plant species in the Maritime Antarctic. Moreover, the experiments set before establishing the Antarctic Treaty on planting other species purposely were unsuccessful [6]. The only survived plant is a hardy cosmopolitan *Poa annua* L., introduced by humans in the small areas at Cierva Point, northern Antarctic Peninsula, and King George Island [6]. Should two native Antarctic plants be regarded under the dispersal concept? Here we try to clarify the subject.

The Antarctic flora in the context of geological events

The main subfamilies of Poaceae evolved and spread over the Gondwana super-continent in the Early Tertiary [9]. The oldest fossil pollen assigned to Caryophyllaceae (*Periporopollenites polyoratus*) was found in Australia and New Zealand and is dated by the Late Cretaceous [10]. Both families had enough time to spread as Gondwana continental plates were connected for a long time after their origin; thus, Australia completely separated

from Antarctica only in the Early Oligocene (about 30 Ma) [3]. It was then that the Antarctic Circumpolar Current formed. Before that Antarctica was also connected to South America [11]. One should assume the mutual contacts of the continents in the Eocene-Miocene and even later, resulting from northward and southward movements of continental plates [9]. Glaciations are known to develop in Antarctica since the Eocene. Polish geologists have recently discovered on King George Island the first Eocene mountain glaciers that preceded major ice sheet formation in Antarctica [12]. West Antarctica also shows a fairly well preserved glacial record exposed on the South Shetland Islands and Antarctic Peninsula [13]. The Paleogene−Neogene strata on King George Island display a sequence of alternating glacial and interglacial events, with at least two regional ice sheet expansions during the Oligocene Polonez Glaciation (32−26 Ma) and the Miocene Melville Glaciation (23−20 Ma) [14]. Despite all these glaciations, in the Pliocene there were tundra complexes with decumbent ligneous *Nothofagus beardmorensis* (Nothofagaceae). There were also cushion-like forms, distantly resembling *D. antarctica* and *C. qiutensis*. However, their taxonomic identity remains uncertain because it is difficult to determine genera using the available fossil remnants [7]. Hence, the initial glaciation occurred at the early stages in opening of the Drake Passage and well before the separation of the South Shetland Islands from the mainland Antarctic Peninsula, about 2 Ma [15]. The simple vegetation communities and low plant diversity observed today contrast with the comparatively rich fossil record. The development of the Antarctic ice sheets resulted in radical changes in vegetation. However, the nature and timing of extinctions caused by climatic cooling are still being debated largely due to the paucity of Neogene fossil sites [8].

Could vascular plants survive Antarctic glaciations?

The concept of polar refugia was developed mainly for the Arctic and other northern regions. As for Antarctica, we have enough evidence for some plants being able to survive the glacial epoch and thrive during subsequent gradual deglaciation [17, 18]. The idea of refugia was at first stated as the so-called nunatak hypothesis [19]; according to it, polar plants could survive on rock eminences protruding from glacial surface, or nunataks.

At the same time, there is some evidence indicating incompleteness of the Antarctic glacial cover. Thus, even when the last glaciation was at its maximum (10−15 thousand years ago), as well as throughout the so-called small glacial epoch (500−100 years ago), there was no ice in one of the largest oases of Eastern Antarctica − the Banger oasis [20].

A number of scientists discuss the possibility for invertebrate animals to withstand glaciation in Antarctic refugia. These are sometimes considered as probable Gondwanan relicts, such as mites, nematodes, and springtails, thought to survive in the refugia of the Trans-Antarctic Mountains [21, 22].

We adhere to the opinion that as the continent gradually cooled and tundra formed, there still could stay vascular plants, not only lichens and mosses. However, their refugia are more likely to be found in the coastal areas of Maritime Antarctic, with the calefactory effect of the Antarctic Circumpolar Current, not nunataks with low humidity and high insolation. Coastal areas represent stone beaches alternated with low rocks that protect vegetation from strong winds and accumulate moisture both from melting ice and humid oceanic air. *D. antarctica* and *C. quitensis* are currently abundant on low coastal territories [6], where their communities are dense and occupy vast areas. A similar situation occurs in the glacial river valleys of King George Island, near the Polish *Henryk Arctowski* station, Barton [23] and Fildes [24] Peninsulas, Livingstone Island (Metcheva, personal communication, 2006), Argentine Islands and nearby archipelagos (Chesalin, personal communication, 2006). The present-day area of these territories is very small in comparison with bare, vegetation-free moraines [8]. Expansion of tundra biomes from the very sites occurs in last decades due to the present climate warming. It is noted in a number of records [5, 23−25].

Are these two species relicts of the Tertiary? Taliev wrote that, without direct paleontology evidence, a rare and isolated species can be referred to as a relict only if it is positively proved that it could not have penetrated and spread there later [38]. Migrations to Antarctica were utterly difficult since the Pliocene, mainly due to the Antarctic

Circumpolar Current and the Polar Front [5, 27]. Even *Acaena* (Rosaceae) and *Uncinia* (Cyperaceae) species have not yet invaded Antarctica, though they have adaptations to be transferred by birds crossing the Drake Passage (*Larus dominicanus* and *Catharacta lonnbergi*) [6].

Genetic aspects

It is commonly considered that divergence of plants and animals is higher in populations of glacial refugia due to their prolonged isolation. This is supposed to permit to distinguish long-settled species from postglacial invaders, the last showing low heterogeneity [18]. In an individual locus, inbreeding, selfing, and vegetative propagation result in genome homogenisation [28, 29]. Thus, sufficient interpopulational heterogeneity was revealed in several separated *Saxifraga paniculata* Mitt. populations of the Alps and other European mountains; it has been shown by combining several techniques (ITS, RAPD and AMOVA-analyses) [30]. Such heterogeneity is often used to verify the relict hypothesis. We came across only one research comparing several *C. quitensis* specimens of Chile and Maritime Antarctic by sequence of rDNA Internal Transcribed Spacer (ITS). Analysis showed 1.17 % sequence heterogeneity [31]. At the same time, ITS-sequences, being transcribed and the most conservative among those of the ribosomal cistron, are commonly used for phylogenetic analysis of species and higher taxa [32]. Estimation of interpopulational heterogeneity, as in our case, would require other methods. For example, RAPD banding in *Saxifraga paniculata* has revealed that 91.2 % of the band were polymorphic, only 8.8 % were scored in all individuals from all populations. At the same time, ITS-analysis obtained 583 base positions of which 14 were variable (2.4 %). Except for one population, all investigated plants from the Southwest and West German populations had identical ITS-sequences [30]. Hence, testing the relict hypothesis of both Antarctic vascular plants should be based on an integral comparative population study in South America and Antarctica. Another question is whether the species are relicts occurring within their natural ranges, or so-called migratory relicts. According to Szafer, a migratory relict is the species being actually relict only in several refugia within its area, having already spread to adjacent territories [33]. The Maritime Antarctic

localities of both species are scattered on separate archipelagos and the coast of the Antarctic Peninsula. Are they parts of the initial South America – Antarctica refugium, or are they themselves independent refugia? Genetic investigations using the AFLP method showed low heterogeneity between spatially isolated populations of *D. antarctica* [34, 35]. The result could arise from the gene flow between populations. Antarctic birds, thought to carry the initial stock of plant seeds [6, 21, 31, 36], seem to play now an important role in interpopulational exchange. Regarding an inclement Antarctic climate since the end of the Pliocene and the isolation, of the continent new species can hardly penetrate there, including even those with special adaptations to transfer of their diaspores by birds. Our own observations, as well as other studies, allow supposing that birds (mainly *Larus dominicanus, Catharacta lonnbergi*, and *C. maccormiki*) are secondary carriers between islands. When they begin nesting, the most of Maritime Antarctic coastal areas but separate plots are covered with ice; that is why birds have to fly from island to island to procure enough green sprouts for building their nests. Edwards considers that new localities were colonised primarily by vegetative propagation, which is promoted by the high tolerance of *D. antarctica* to periods of uprooting and its ability to re-establish itself [37]. Gerighausen et al. [24] suggest that the expansion is a direct consequence of regional warming, possibly promoted by birds or other factors. This enables further expansion and breaks the genetic isolation; populations become homogeneous to a certain extent. To summarize all aforesaid, we suggest that both species could survive throughout glaciations in the most protected loci – refugia, and later they spread locally to adjacent ice-free territories. The main dispersal factor is birds, and the plants themselves are migratory relicts.

Conclusions

Present-day distribution patterns of *Deschampsia antarctica* and *Colobanthus quitensis* in South America and Antarctica are likely caused both by factors of vicariance-based and dispersal-based schemes. The species could have migrated to Antarctica in the Oligocene-Pliocene, not in the Holocene. Before the Antarctic Circumpolar Current has formed, new families of herbaceous plants passed through Antarctica via a land bridge bet -

ween South America and Australia, for the continent was much less isolated from South America. The dissemination could take place both through intercontinental bridge and due to bird transfer, as birds such as skuas were closely connected with penguin colonies, the latter inhabiting Gondwana remnants since the end of the Cretaceous. Successful naturalization of the species in Antarctica could occur only when climate was relatively favourable; nowadays they reveal amazing stability due to gradual adaptation to habitat deterioration in the Pliocene. We suggest that other vascular plants cannot survive in Antarctica because they lack such adaptability. Climate warming enables *D. antarctica* and *C. quitensis* to extend from coastal refugia to adjacent islands and oases. Perhaps once it was so in South America (e.g., *C. quitensis* nowadays is found northward to Mexico [28]). Because of that we consider these species migratory relicts.

РЕЗЮМЕ. Сегодня существует загадка распространения в Антарктике только двух видов сосудистых растений − *Deshampsia antarctica* и *Colobanthus quintesensis*. Даже в условиях прогрессирующего потепления в регионе зафиксировано распространение только одного адвентивного вида при прямом участии человека. Исходя из данных об истории биоты и оледенений в Антарктике, сделана попытка объяснить такую ситуацию проникновением обоих видов в Антарктику на временном отрезке олигоцен−плиоцен, в момент меньшей изоляции Антарктики и более благоприятной для натурализации климатической ситуации. Существенное внимание уделено генетическим исследованиям обоих видов. Современные данные дают возможность говорить о вторичном расселении видов в антарктическом регионе, что наблюдается и в последние десятилетия. Ему благоприятствуют наблюдаемые климатические изменения и птицы в качестве переносчиков. С учетом этого выдвинута гипотеза о том, что *D. antarctica* и *C. quintesensis* являются миграционными реликтами.

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