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RESEARCH

Umbilicaria africana (*Umbilicariaceae*, lichenized fungi) new to the Arctic and a hypothesis for its bipolar distribution

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Abstract

Umbilicaria africana, hitherto only known from Africa, South America, Antarctica, and the Malay Archipelago in Southeast Asia is reported from the West Chukotkan sector of the Arctic and North Eurasia as whole. Morphological details of the Arctic material are provided. *Umbilicaria aprina* is excluded from the flora of the Chukotkan sector of the Arctic as a previous erroneous identification of the specimen of *U. africana*. The bipolar distribution of *U. africana* is discussed. Based on analyses of migratory bird species composition and their ecology in localities where arctic-alpine *U. africana* was collected, we suggest that the Northern Wheatear (*Oenanthe oenanthe*) might play an important role in the long-distance dispersal of specific propagula (thalloconidia) of *U. africana* from East Africa, and the Arctic Warbler (*Phylloscopus borealis*), the Eastern Yellow Wagtail (*Motacilla tschutschensis*), or less probably the Pechora Pipit (*Anthus gustavi*), from Australasia (Malay Archipelago).

Keywords Biogeography · Bipolar distribution · Russia · Thalloconidia · West Chukotka

Introduction

Lichens are symbiotic phenotypes resulting from the interaction of a fungal partner, the mycobiont, and one or more photosynthetic partners, the photobiont. Lichens show distinctive patterns of distribution, similar to other major groups of organisms. Some lichens appear to have very restricted ranges; others are extremely widely distributed, whilst most have ranges between these two extremes (Feuerer and Hawksworth 2007; Galloway 2008; Werth 2011; Arcadia 2013; Feuerer and Höhne 2017). Compared to other organisms, such as vascular plants or mosses, lichen-forming fungi have a high number of species with so-called bipolar or amphitropical distributions, i.e. occurring in both the northern and southern hemispheres, but are largely absent from intermediate, tropical latitudes (Du Rietz 1926, 1940; Oksner 1944; Galloway and Aptroot 1995; Garrido-Benavent and Pérez-Ortega 2017). Few bipolar species, however also occur at high elevations at latitudes closer to the equator, or even wider. For example, the subcosmopolitan bipolar species *Cetraria aculeata* (Schreb.) Fr. is common in high alpine mountain belts in tropical Africa and South America (Lutsak et al. 2016). This species has an exceptionally broad ecological niche and distribution and is often found in open polar, high mountain and boreal environments, in forest gaps, steppe and coastal ecosystems from the maritime Antarctic to the high Arctic, including Mediterranean and Temperate zones (Kärnefelt 1986; Fernández-Mendoza and Printzen 2013; Lutsak et al. 2016).

Umbilicaria africana (Jatta) Krog et Swinscow represents a rare distribution pattern being common in tropical high mountains of Africa, South America and Southeast Asia, as well as in Antarctica, but hitherto has not been reported for the Arctic and Northern Hemisphere north of Ethiopia and Mexico. This taxon was described as *Gyrophora haplocarpa* var. *africana* Jatta from the alpine belt of Ruwenzori Mts, Uganda [elev. 4000–4500 m] (Jatta 1908). Krog and Swinscow (1986) raised the taxon to the species level as *Umbilicaria africana* and revealed that thalloconidia septation was

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an important diagnostic trait for distinguishing it from *U. aprina* Nyl., which has similar morphology and ecological preferences. Thalloconidia are mitosporic thick-walled, dark-coloured dispersal units, developed by the mycobiont and shed mainly from the lower cortex and/or the rhizinomorphs (Hasenhüttl and Poelt 1978; Hestmark 1990). Thalloconidia are rather characteristic for *Umbilicaria* and few other genera and can be non-septate or septate and were shown to be highly species-specific (Krog and Swinscow 1986; Hestmark 1990, 1991a, b, c; Krzewicka and Flakus 2010). Thalloconidia of *U. africana* are 4–10 septate, whilst in *U. aprina* they are simple or one-septate. Hestmark (1991a) during his extensive study of thalloconidia in *Umbilicariaceae* proved the reliability of this trait for the circumscription of *U. africana*. For a long time *U. africana* was known only from the type locality. Almost a century after the original description by Jatta (1908), Krog and Swinscow (1986) reported the species for high mountains of Ethiopia (Bale Mts, Semien Mts), Kenya (Mt Kenya, Mt Elgon), Tanzania (Mt Meru, Kilimanjaro), and Uganda (Ruwenzori Mts, Muhavura) and considered the species endemic for East Africa. The species was, however, discovered later in Antarctica (Sancho et al. 1992; Øvstedal and Lewis Smith 2001; Krzewicka and Smykla 2004; Giginiak et al. 2016; Krzewicka et al. 2024), South America (Colombia—Sipman and Topham 1992; Venezuela—Marcano and Morales Méndez 1994; Chile—Galloway and Quilhot 1998; Bolivia—Hestmark 2009, Krzewicka and Flakus 2010; Ecuador and Perú—Hestmark 2016), Mexico (Herrera-Campos et al. 2020) and in the tropical islands of South Asia (Kalimantan—Sipman 1993; Java—Wei and Jiang 1993). According to a phylogenetic study by Davydov et al. (2017), *U. africana* belongs to the '*U. aprina*' group within *Umbilicaria* subg. *Umbilicaria*, which includes several closely related species, i.e. *U. africana*, *U. antarctica* Frey et Lamb, *U. aprina*, *U. formosana* Frey, *U. kappeni* Sancho et al., *U. krascheninnikovii* (Savicz) Zahlbr., and *U. rhizinata* (Frey et Poelt) Krzewicka.

Umbilicaria africana has been included in the Lichen Flora of Russia (Davydov 2017) without adequate documentation in the scientific literature. Here we amend this inaccuracy and discuss in detail the occurrence of *U. africana* as a new record for the Arctic, reported here from the West Chukotka sector, ca. 162–180º E (see Kristinsson et al. 2010). The distance between the new locality and known populations is 8000 km (Malay Archipelago) or 11,500 km (East Africa). Disjunct distributions over wide areas are known for lichens including some species of *Umbilicaria* (Wei and Biazrov 1991; Codogno 1995). Like other groups of fungi, the wide disjunctions may indicate either extremely old age of the species (before Pangea and Gondwana broke), or their narrow environmental specialization and effective long-distance propagule dispersal. According to a molecular clock analysis (Prieto and Wedin 2013), *Umbilicariales* branched off from the main lineages of *Lecanoromycetes* prior to the major diversification of the latter ca. 191 million years ago (Ma), but lichen species in general and species of *Umbilicariaceae* in particular seems to be too young in evolutionary terms for plate tectonics to have shaped their current disjunct distribution, as has been suggested for high-ranking taxa (Galloway and Aptroot 1995; Arcadia 2013). Vectors such as wind, water, and migratory animals, have been traditionally thought responsible for direct long-distance dispersal of lichen propagules (e.g., Søchting and Castello 2012; Garrido-Benavent and Pérez-Ortega 2017; Torres et al. 2023 for a review). Ascospores of many fungi including lichens are small, which allows a long-distance dispersal (Wilkinson et al. 2011). This idea is supported by DNA surveys based on aerial samples (Ovaskainen et al. 2019). Lichens have a stronger association of floristic similarities with maximum wind connectivity than with geographical proximity (Muñoz et al. 2004). This fact well explains circumpolar distribution of many species of lichens, but it seems unlikely that airborne lichen propagules could cross the Intertropical Convergent Zone (Wilkinson et al. 2011). Birds are widely recognized as important dispersal vectors of seeds (see Viana et al. 2016 for a review) and have been implicated as responsible for bipolar distributions of lichen-forming fungi (e.g. Geml et al. 2012; Søchting and Castello 2012; Garrido-Benavent et al. 2017). Davydov et al. (2019) suggested that migratory birds may play an important role in the long-distance dispersal of bipolar species of *Umbilicaria* reproducing mostly by thalloconidia (i.e. *U. aprina*, *U. decussata* (Vill.) Zahlbr., *U. cinerascens* (Arnold) Frey, *U. polyphylla* (L.) Baumg., *U. subpolyphylla* Oxner, and *U. africana*). Indeed, thalloconidia have thick cell walls (Hasenhüttl and Poelt 1978; Hestmark 1991a; Ascaso et al. 1992), which are presumed to be more resistant to adverse environmental conditions for a longer time than thin-walled ascospores (Hestmark 1997); thus, thalloconidia could be more effective than ascospores in long-distance dispersal of *Umbilicaria*. Birds in general are mentioned by researchers as a possible agent of fungal long-distance dispersal. We evaluated potential bird species linking *U. africana* populations widely separated from each other for thousands of kilometres in the Asian Arctic and other habitats in the Northern and Southern hemispheres. The goal of our study was to explain the most likely origin of the Arctic population of *U. africana*.

Material and methods

To examine morphology and distribution of the species, herbarium specimens were studied from the herbaria CANB, FH, FR, G, GZU, H, HMAS, HUH, LE, M, MIN, SNP, and private collections from Chile and Antarctica.

Morphological observations were made using a dissecting microscope. Measurements are presented as follows: (smallest value recorded) (x-SD)—x—(x + SD) (largest value recorded), where x is the (arithmetic) sample mean, and SD the sample standard deviation. The total number of samples measured (*n*) are given in parentheses. The two extremes are given to the nearest 0.5 µm, and the sample mean to the nearest 0.1 µm.

We tried to extract DNA and amplify the nuclear ribosomal Internal Transcribed Spacer (ITS) from Arctic specimens to get additional molecular and phylogenetic data, but were not successful, due to the age of the specimens collected in 1977. We used scanning electron microscope (SEM) to visually compare thalloconidia of our specimens with the morphologically related *U. rhizinata*. Microphotographs were obtained using a Carl Zeiss EVO MA 10 SEM. The samples were dried in air, fixed on aluminium stubs with double-sided sticky film, and then gold was sprayed on them.

To test the possibility of a long-range latitudinal transfer of thalloconidia by birds, we evaluated potential migratory species. For this purpose, published lists of birds of Chukotka with descriptions of migration routes (Portenko 1981; Kischinsky 1988), Central and Eastern Africa (Stevenson and Fanshawe 2001; Redman et al. 2011), Northern Kalimantan (Davison 2016) were analyzed. For several species selected by us according to the criteria described below, samples were retrieved from the GBIF system based on their registration in the vicinity of the *U. africana* habitats, which makes it possible to estimate the probability, as well as to some extent, the frequency of visits by these species to these places. We did not consider possible long-distance migration of *U. africana* directly between Arctic and South America or Antarctica, since there is not a single species of bird living on the territory of Chukotka, remote from the coastline, which could regularly reach these continents. We accepted the following criteria for bird species: (1) It is known to nest in Chukotka. (2) It is known to winter in regions where *U. africana* is recorded (Fig. 1). Hence, we primarily considered Arctic-Alpine species that live both in the circumpolar and mountain tundra, respectively, having, amongst other traits, a tendency to stay and feed on wintering grounds in similar landscapes. (3) It feeds on the ground, because birds feeding in water or air are less likely to link habitats of saxicolous lichens.

Results

Taxonomy

Umbilicaria africana **(Jatta) Krog et Swinscow**

1986, Nordic J. Bot. 6(1): 79. ≡ *Gyrophora haplocarpa* var. *africana* Jatta 1908, Ann. Bot. (Roma) 6: 408. ≡ *Omphalodiscus africanus* (Jatta) Llano, 1950, Monogr. *Umbilicariaceae*: 99.

Type: [Uganda, Ruwenzori Mts.] “versante ovest Duroni, 4000–4500 m, det. Jatta” s. n. (Lectotype designated by

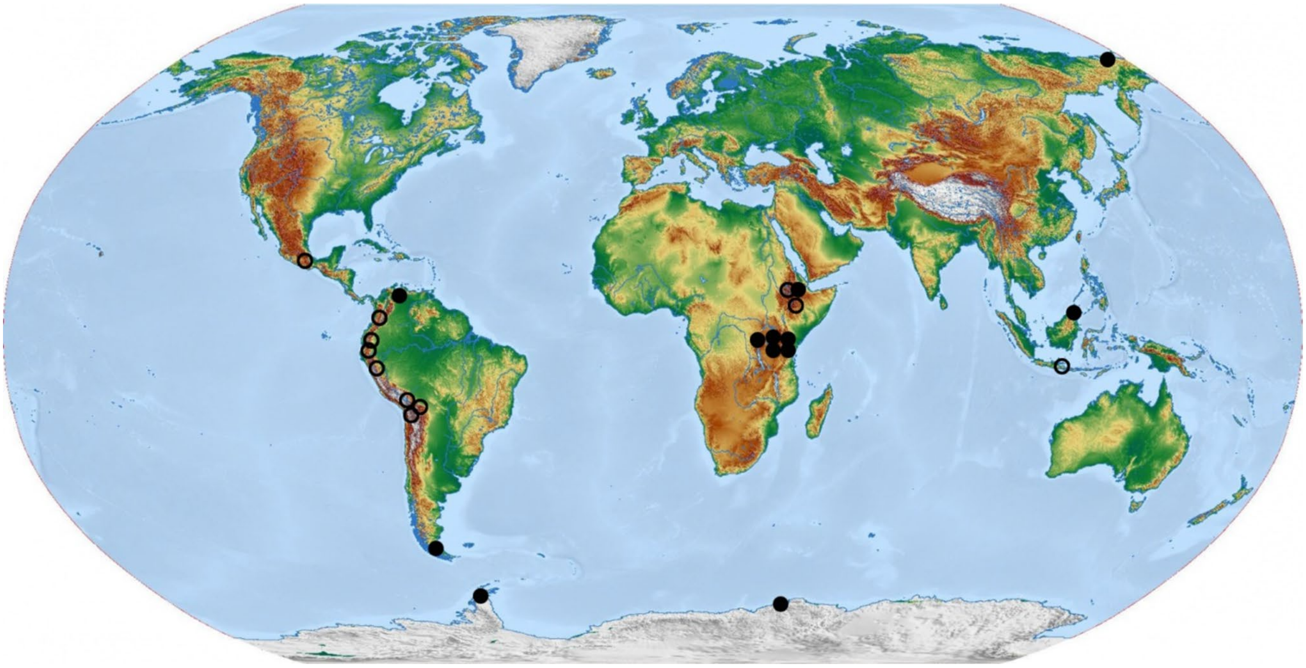

Fig. 1 The distribution of *Umbilicaria africana* ●—examined specimens; ○—literature data

Davydov and Yakovchenko (2023, 2024), NAP, Jatta collection [high resolution digital photos!]).

Morphology, anatomy and secondary chemistry

The morphological description of the species is available in literature (Krog and Swinscow 1986; Krzewicka and Smykla 2004; Hestmark 2016). The North Asian Arctic specimens are represented by several relatively small 4–8 mm in diameter thalli with greyish upper surface and dark marginal rhizinomorphs giving a ciliate appearance; lower surface covered by thalloconidia and black at the central part, and gray at periphery with pale gray rhizinomorphs developed mostly at peripheral part of lower surface (Fig. 2). Thalloconidia developing on the lower surface are multicellular from 4 cells to more, often (6–)8–12–16(–24) cells ($n = 30$). The size of 4-cells thalloconidia is (12.5–)14.1–15.5–16.9(–17.5) × (12.5–)12.5–13.4–14.5(–15.0) µm ($n = 20$): the size of thalloconidia when the number of cells is more than 4 is (18.0–)19.5–22.3–25.0(–30.0) × (13.3–)15.5–17.7–20.0(–27.5) µm ($n = 20$) (Fig. 3, 4). The size of thalloconidia is similar to those of syntypes from Ruwenzori Mts.: (17.5–)18.6–22.2–23.7(–27.5) × (13.8–)15.6–17.6–19.7(–22.5) µm [$n = 20$, only thalloconidia more than 4 cells were measured] (HUH 940412), and (17.5–)19.2–20.7–22.2(–27.5) × (15.0–)16.7–18.3–20.0(–22.5) µm [$n = 20$, only thalloconidia more than 4 cells were measured] (MIN 663399).

Apart from the small size, the specimens from Russia fit well with the conception of *Umbilicaria africana* by having multicellular thalloconidia and marginal rhizinomorphs. The average thallus size of *U. africana* is usually about 3–6 cm in diameter, whilst African specimens sometimes reach 14 cm in the diameter (Krog and Swinscow 1986). However, specimens from Java Is. are also relatively small, ca. 1.5 cm in diameter (Wei and Jiang 1993: 68, Fig. 37). The closely related species *U. rhizinata* is also small (0.8–1.5 cm) but differs in having 2–4-celled thalloconidia and lacks marginal rhizinomorphs. Thalloconidia of *U. africana* are considerably larger than of *U. rhizinata* (Figs. 3, 4, see also Fig. 2 in Davydov 2022). The small size of the Russian thalli of *U. africana* might be due to either harsh climatic conditions or by the young age of the sampled population.

Distribution

Umbilicaria africana has a scattered distribution based on specimens examined from almost all known locations in ten countries and Antarctica (black dots, Fig. 1). In addition, we checked literature data (see Introduction) and corresponding photos and label data of specimens provided by the Consortium of Lichen Herbaria (2023).

Specimens examined **Russia**, Chukotka Autonomous Area, northern part of Anyuiskoye Upland, middle section of Kytep-Guitenryveem River, canyon at the upper reaches of the Baranij Creek, at watershed, [69º 18′ N, 165º 01′ E, elev. ca. 350 m], 22 VIII 1977, *M. P. Andreev* (LE L5326!).

Additional specimens examined **Ethiopia**, Amhara region, North Gondar zone, Debarq woreda, Simien Mts. National Park, road from Chennek Base Camp to Mt. Bwahit, ca 750 m SW of summit of Mt. Bwahit, alpine stand of *Lobelia rhynchopetalum*, in rock crevices, 13° 14.457′ N, 38° 12.728′ E, elev. 4260 m, 16 II 2014, *T. Lutsak* (FR 220099!). [**Kongo**] Zaire (Africa centralis), Prov. Kuvu: ad latera septentrionalia montis ignuvomi Karisimbi, ad lapides parvos vulcanicos in regione subnivali, elev. 4450 m, 26 I 1972, *J. Lambinon* 72/452 (LE L5606!). Ruwenzori, Vorfeld des Glacier Stanley Occidental, 4300 m, an amphibole-trachy-Andesit Blöcken, 1956, *R. E. Besdul* (G 00111730!). **Uganda**, [Ruwenzori Mts.], "versante ovest Duroni, 4000/4500″ (HUH 00940412!); [Uganda] "Ruwenzori, veyante orest Duvoin 4–4500 m" (MIN 663399!). Ruwenzori, the Mt Stanley area, 4500 m, 1952, *E. Bergström* 109a (H!); same locality, *E. Bergström* 98a (H); same locality (HMAS-L 005455!). Ruwenzori Mts., Mijusi Valley, Eastern slope of Mt. Speke, elev. 4530 m, on stones in a small stream, 29 III 1948, *O. Hedberg* 581 (H 5523!). **Tanzania** ("Tanganyika Territory"), Mt. Meru, Eastern slopes above Olkakola estate, alpine region, on rocks immediately below the summit, 3° 14′ S, 36° 45′ E, elev. 4,500 m, 28 X 1948, *O. Hedberg* (CANB!). **Kenya**, Mt Kenya, Western alpine region, on the moraine ridge south of Lewis glacier; on a big boulder about 400 m from the glacier, elev. 4,700 m, 17 VIII 1948, *O. Hedberg* (HMAS L005453!). Mt. Kenya, alpine region, Teleki Valley near the edge of Tyndall glacier, on boulders, 4,500 m, 29 VII 1948, *O. Hedberg* 1737 (HMAS L5454!). Aberdare Mts.: Satima, 4000 m, on rock, 22 VII 1986, *K. Schmitt* (M 0059141!). **Malaysia**, Borneo, Sabah, Mt. Kinabalu, Low Peak, elev. 4100 m, *H. Sipman* (SNP!). **Venezuela**, Anden, Estado Mérida: Sierra Nevada do Merida, Pico Espejo, 4,750 m, 11 XII 1968, *B.* and *F. Oberwinkler* (M!); Sierra de Santo Domingo, Páramo de Mucubaji: Höhen oberhalb der Straße nach Pinango, ± 1 km NW der Pabhohe El Aguila" (4,180 m), 28 III—07 VII 1969, *H. Hertel, B.* and *F. Oberwinkler* (M!). **Bolivia**, Prov. La Paz Cordillera Real, Ostseite des Zongopaβ auf Silikat, 4,700–4,800 m, 14 III 1969, *H.* und *H. Doppelbaur* (GZU!). **Chile**, XII Region. Isla Grande de Tierra de Fuego. Glaciar Pia. Bloques en la playa. Sobre rocas 54° 46′ 43″ S, 69° 35′ 15″ W, elev. 1–5 m, 14 XII 2009, *S. Pérez-Ortega* 1774 (hb. Pérez-Ortega, ALTB L5466!). **East Antarctica**, Enderby Land, Tala Hills, the area of the "Vechernaya Mountain" basecamp, 67° 39′ 26.0″ S, 46° 09′ 57.0″ E, elev. 38 m, 2013, *V. E. Miamin* (ALTB–L5503!). **West Antarctica**, South Shetland Islands. King George Island, Admiralty Bay area:

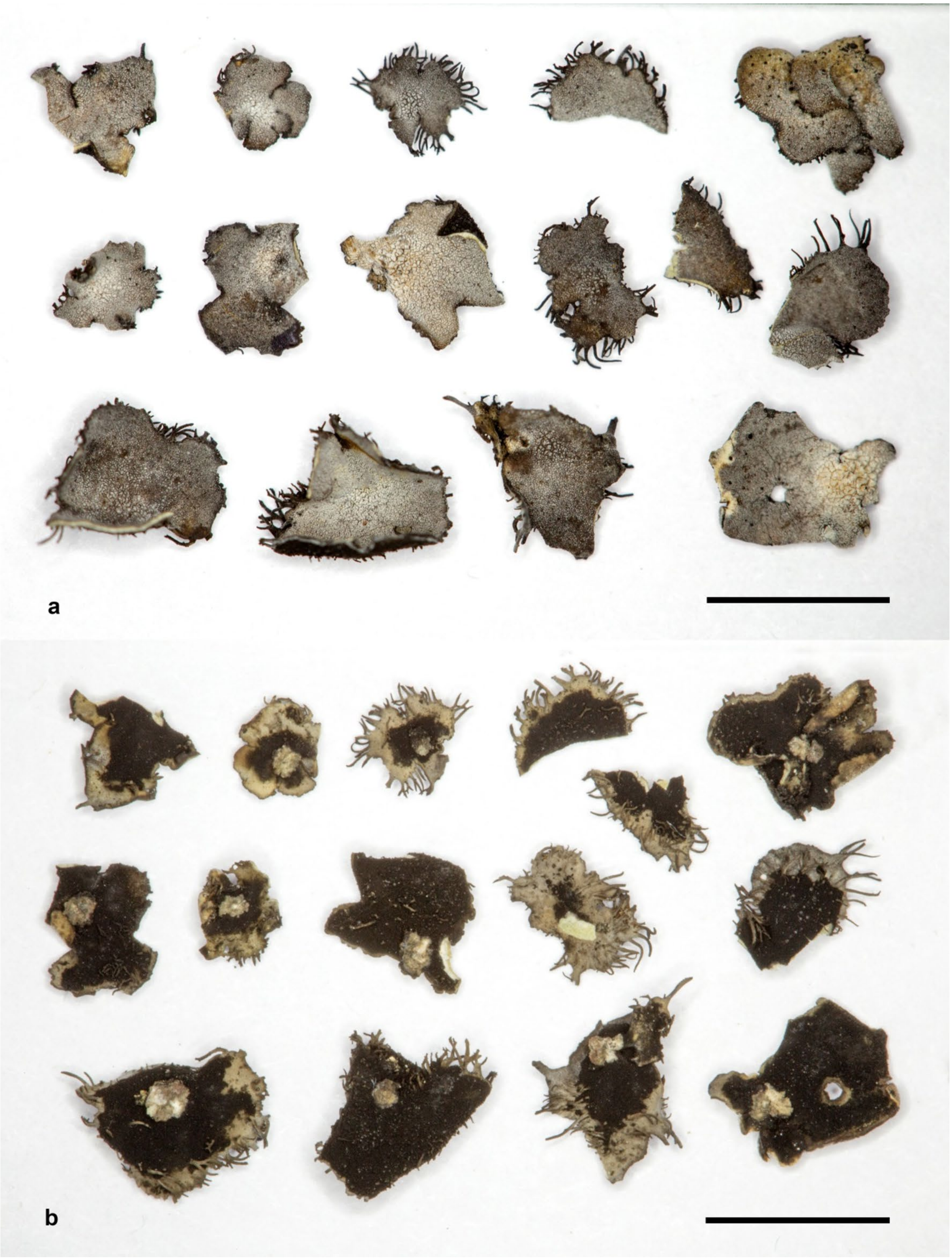

Fig. 2 Specimens of *Umbilicaria africana* from Arctic Chukotkan sector (LE-L5326). **a** Upper thallus surface. **b** Lower thallus surface. Bars = 5 mm

Ore Point on west coast of Keller Peninsula, Mackellar Inlet, 62º04′20″S, 58º25′30″W, elev. 8 m, 9 I 1980, *R. Ochyra* 526/80 (H!).

Migratory birds

Our selection criteria revealed a relatively small number of bird species that nest in West Chukotka and spend a part

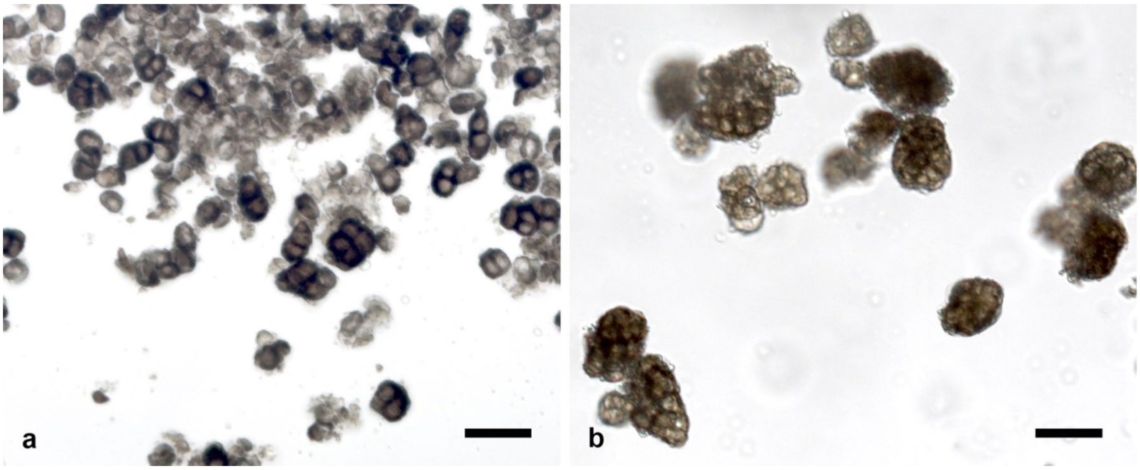

Fig. 3 Thalloconidia of *Umbilicaria rhizinata* and *U. africana* (light microscopy). **a** *U. rhizinata* (MIN-664956). **b** *U. africana* (LE-L5326). Bars = 20 µm

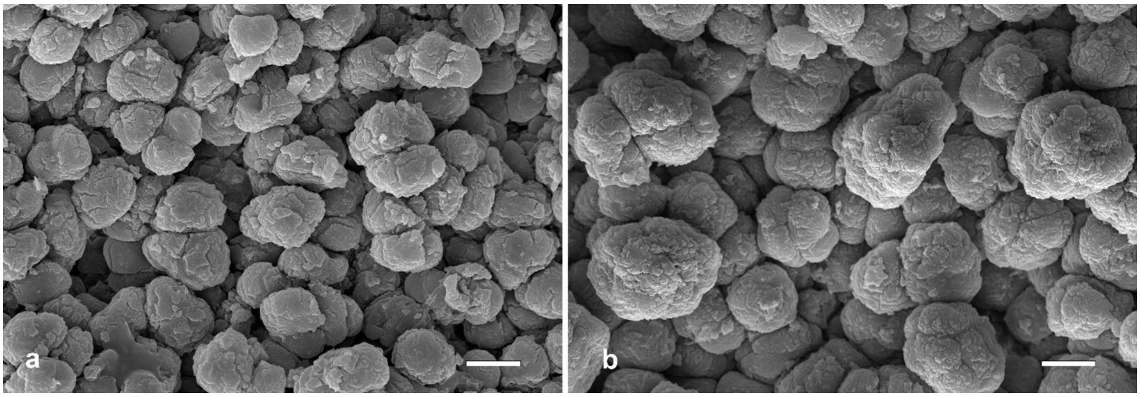

Fig. 4 Thalloconidia of *Umbilicaria rhizinata* and *U. africana* (SEM) **a** *U. rhizinata* (Davydov 7258 [ALTB]). **b** *U. africana* (LE-L5326). Bars = 10 µm

of the year wintering in other regions, including *Umbilicaria africana* habitats. For the African continent, the only species that meets our criteria is Northern Wheatear, *Oenanthe oenanthe* L., which breeds everywhere on Chukotka (Portenko 1981), and winters in Central and Eastern Africa, where it is indicated as a common and widespread species climbing mountains to the elevation up to 3600 m (Stevenson and Fanshawe 2001; Redman et al. 2011). We also considered the option of migration along the East Asian—Australian migration route by species wintering in the eastern regions of Southeast Asia, including the Malaysian archipelago. Here, the main agents can be the Arctic Warbler, *Phylloscopus borealis* (Blasius), breeding in the eastern and inner parts of the Chukotka, found on the coast only during by-flights (Portenko 1981), the Eastern Yellow Wagtail, *Motacilla tschutschensis* (JF Gmelin), breeding everywhere in Chukotka (Portenko 1981) and to a lesser extent the Pechora Pipit, *Anthus gustavi* (Swinhoe), breeding in the inner Chukotka Peninsula (Portenko 1981). The Arctic Warbler and the Eastern Yellow Wagtail are regularly observed in the mountainous part of Northern Kalimantan according to GBIF; the migration of Arctic Warbler from the Malay Archipelago to the Arctic has been documented using individual tracking (Adams et al. 2022). The Pechora Pipit is mainly a coastal species, but its flights into the mountains cannot be excluded.

Discussion

The studied specimen from Chukotka was reported by Andreev (1984) as *Umbilicaria canescens* Dombr. but was not included in the final checklist (Andreev et al. 1996) because authors followed Santesson (1993) who treated *U. canescens* as *U. cylindrica* (L.) Delise ex Duby var. *delisei* Nyl. Davydov Zhurbenko (2008) and Kristinsson et al.

(2010) erroneously reported the same specimen as *U. aprina* (Davydov 2022). The latter species therefore should be excluded from the list of species of West Chukotkan sector of the Arctic. Specimens from the Arctic are rather small. In the wet Ruwenzori Range, it reaches its largest size, up to 14 cm in diameter (Krog and Swinscow 1986), whereas thalli collected on Java Is. are much smaller (Wei and Jiang 1993: 68).

The distribution of *U. africana* is highly disjunct (Fig. 1), occurring in high alpine and polar habitats. It is also the most common high alpine *Umbilicaria* species on siliceous rock boulders in African tropical high mountains ranging from 3000 to 5000 m (Krog and Swinscow 1986) and of South America [mainly 4400–5000 m] (Hestmark 2016). In the Kalimantan Is., *U. africana* is a rare species with a distribution restricted to the summit area (ca. 4000 m) of Kinabalu Mt. (Sipman 1993). In maritime Antarctica the species is rare, though locally abundant, and usually found inland at elevations 25–200 m a.s.l. on vertical, north-facing rocks, growing amongst other species of *Umbilicaria* (Sancho et al. 1992; Krzewicka and Smykla 2004; Krzewicka et al. 2024).

The currently known range of *U. africana* does not follow any known distribution pattern of lichens (Galloway 2008). Some other bipolar Arctic-alpine-Antarctic species, e.g. *U. aprina* or *U. decussata*, are much more widespread, and *U. africana* has not been found in the same localities as these species. The most phylogenetically related species, *U. aprina*, requires similar environmental conditions, but has a considerably wider distribution and occurs in almost all high mountains with glaciers (Crespo and Sancho 1982; Hestmark 1997, 2016; Davydov et al. 2024). *Umbilicaria decussata* is distributed even more widely than *U. aprina* (Wei and Jiang 1993).

According to the model of the global atmospheric circulation by Wilkinson et al. (2011), extensive within-hemisphere wind dispersal of propagules above a diameter of 20 µm between continents becomes increasingly unlikely. Most thalloconidia of *U. africana* are multicellular and larger than 20 µm. In contrast to *U. africana*, *U. aprina* and *U. decussata* possess mostly non-septate thalloconidia ca. 6.0–7.5 µm in size. Thus, wind may be an important long-distance dispersal vector for *Umbilicaria* species with a small thalloconidia, but wind might not effectively spread larger thalloconidia, as in *U. africana* or *U. polyphylla*, consistent with Tibell's (1994) finding that *Caliciales* species with larger ascospores have significantly narrower ranges compared to species with small ones. *Umbilicaria africana* can also produce ascospores of 10–15 × 5–9 µm, but the restricted distribution of the species suggests that colonization by ascospores appears to be unsuccessful for some reason. A study of 845 herbarium specimens of *U. africana* larger than 5 mm showed that 71.5% had thalloconidia only, 22.8% had both thalloconidia and apothecia, 2.6% had apothecia only, and 3.1% had neither thalloconidia nor apothecia (Hestmark 1991b). Asci of *U. africana* are often immature (Wei and Jiang 1993); in general, the significance of propagation by ascospores is lower in *Umbilicaria* species with thalloconidia or lichenised propagules (Hestmark 1991b, c).

Thus, we infer that long-distance dispersal by thalloconidia via migrating birds is the most plausible explanation for the observed distribution patterns. We cannot exclude the possibility that thallus fragments were also dispersed by birds, but the lack of specialized lichenized propagules and the long distance between sites make this hypothesis less plausible. Within the modern fauna, only a few species of birds could bring thalloconidia between high mountain and Arctic habitats of *U. africana*, and the existence of such species supports our hypothesis.

In the absence of fossil remains and molecular phylogenetic data, we cannot determine exactly when *U. africana* entered the Arctic. In the Old World, habitats for *U. africana* have existed in the East African Mountains since before the Pleistocene, as glaciation was mountainous, with glaciers reaching their maximum 42 to 28 thousand years before the global Last Glacial Maximum. The local maximum was accompanied by a downward shift of the Afroalpine vegetation belt by about 700 m, and its area was larger than it is today (Groos et al. 2021). *Umbilicaria africana* is now widely distributed in the eastern part of Africa (Krog and Swinscow 1986). The species is rare in Chukotka and Australasia, and lichen communities here are relatively young and became suitable for *U. africana* only after the Last Glacial Maximum. The Arctic region as well as Antarctica were subjected to glaciations during the Pleistocene. The Kinabalu Mt. on Kalimantan Is. is a very young geologically and a fast-rising mountain; only its central part is composed of granite, suitable for *U. africana,* and absent from the surrounding areas (Hall et al. 2009). The central part of Kinabalu Mt. as well as other high mountains of Malay Archipelago were subjected to glaciations during the Pleistocene (Hope 2004). The restricted lichen flora at high elevation of Kinabalu Mt. suggests that the modern vegetation has had little time to colonize (Sipman 1993; Paukov et al. 2017). However, in the Arctic and Australasia, *U. africana* may have existed before glaciation and survived the Pleistocene, migrating regionally and persisting in refugia at lower elevations in the surrounding area or on unglaciated ridges.

Long-distance migration patterns of extant bird species have been fairly well studied (Steinbacher 1951; Berthold 2001). Birds nesting in the Asian Arctic, including the Chukchi Peninsula, migrate mainly along the East Asian-Australian migration corridor and winter in Southeast Asia (most species), some aquatic birds follow the northern 'latitudinal' path along the Arctic Ocean, a small number of species migrate along the East Asian-African migration path, reaching wintering sites in Africa (Portenko 1981;

Kischinsky 1988; Ostapenko 1985). The original mechanisms of migration (physiological, behavioural and genetic) have evolved deep in the avian lineage and its expression may change as a function of environmental conditions and is well explained by current climatic factors (Alerstam 2003; Somveille et al. 2018, 2020). Phylogenetic analyses have generally found high rates of transition between sedentary and migratory behaviours, and vice versa (Zink 2011; Winger et al. 2014). Authors proposed the hypothesis that the last glaciation could have shifted the migratory behaviour and migratory routes of some North American species (Winger et al. 2014; Zink and Gardner 2017), which may have lost their migratory condition to recover it later. Somveille et al. (2020), based on simulations at the avifauna scale, suggest an origin of migration on a much longer timescale than the glacial cycles of recent Earth history. Furthermore, the magnitude of the avian response in terms of migratory behaviour to past global change was likely to have differed between the Americas and the Old World. North America predicted to have experienced the greatest changes in bird migration over the last 50,000 years, whereas in the Old World this is somewhat less pronounced, and the Ice Age had little effect on the proportion of species that migrated or on the average distance of migrations (Somveille et al. 2020). Thus, migratory bird connectivity between Africa, Australasia and the Arctic has been maintained for at least the last 50,000 years, but likely much longer. Finlayson et al. (2012), analyzing fossil avifaunas showed that at least 58% of the Middle Pleistocene bird species were already present in the Early Pleistocene records, and the most genera and species of European birds in the Middle Pleistocene between 1.2 and 0.5 million years ago survived into the Late Pleistocene, and even to the present day. The available bird fossil record for the Plio-Pleistocene, covering Eurasia and Africa, suggests that although the species composition of migratory birds has changed, most Palaearctic-Palaeotropical long-distance migratory species now migrate along routes and between regions that were likely established during the Pleistocene or earlier (Finlayson et al. 2012; Ponti et al. 2020).

Phylogeographic studies of amphitropical lichens based on molecular data have been few so far; based on extensive worldwide sampling of *Cetraria aculeata, Pseudephebe minuscula* (Arnold) Brodo et D. Hawksw. and *Thamnolia* species, the timings of disjunctions in these species are generally estimated to be Neogene-Pleistocene (Printzen et al. 2013; Onuţ-Brännström et al. 2017; Garrido-Benavent et al. 2021). The aforementioned species are now more widespread than *U. africana* and reproduce mainly by fragmentation, but it seems plausible that the Neogene-Pleistocene with several glacial periods was a trigger for the diversification and distribution of other arctic-alpine lichens, including *U. africana*. We cannot fully extrapolate these data to the distribution history of *U. africana* until molecular phylogenetic evidence is available, but downward shifts of alpine vegetation in the mountains during glaciation made its area larger than it is today, generally increasing the probability of colonization by propagules carried by migratory birds inhabiting the same environments.

Reproduction of *U. africana* by thalloconidia or ascospores requires the presence of a suitable photobiont in the habitat to be colonised. Accordingly, long-distance dispersal of mycobiont diaspores can only lead to the formation of lichen thalli if the mycobionts are able to use local photobiont pools (Beck 1999; Beck et al. 2002; Blaha et al. 2006). The photobiont of *Umbilicaria* belong to the genus *Trebouxia* (Beck 1999; Romeike et al. 2002; Sadowska-Des et al. 2014). Lichens with *Trebouxia* photobionts are nearly ubiquitous; some *Trebouxia* species seem to occur predominantly in cold climates, e.g. at high altitudes or latitudes, whilst others are rare under such conditions (Blaha et al. 2006; Muggia et al. 2014; Leavitt et al. 2015; Kosecka et al. 2022). Leavitt et al. (2015) suggested that the fungal host genus determines the identity of the algal partner more than ecology at the ecoregions scale. Interactions between potential lichen symbionts are usually described in terms of selectivity and specificity. In the approach proposed by Beck et al. (2002) selectivity is the range of potential photobionts selected by the mycobiont. In temperate and tropical regions, lichens tend to be highly selective towards the photobiont (Beck et al. 2002; Hauck et al. 2007). Studies of *Umbilicaria* and other lichens from polar regions have shown a general tendency towards lower mycobiont selectivity of the photobiont (Romeike et al. 2002; Domaschke et al. 2012; Pérez-Ortega et al. 2012; Jones et al. 2013).

The widely distributed species *U. aprina* and *U. decussata* might have different mycobiont selectivity within the same region. For example, in Antarctica *U. aprina* showed no variation in the species diversity of its photobionts and was primarily associated with a most widespread haplotype (Pérez-Ortega et al. 2012; Jones et al. 2013). In comparison, *U. decussata* photobionts showed very high haplotype diversity (Romeike et al. 2002; Jones et al. 2013). In a study of mycobiont and photobiont of *Cetraria aculeata* in tropical alpine regions of East Africa and South America, *Trebouxia* populations were amongst the most diverse and similar in composition to polar populations (Lutsak et al. 2016). It is possible that mycobionts from polar and alpine environments utilize local photobionts, which may also be better adapted to the local environment, rather than being restricted to a specific photobiont (Romeike et al. 2002; Fernández-Mendoza et al. 2011; Pérez-Ortega et al. 2012; Lutsak et al. 2016). Lower selectivity may also be a direct consequence of surviving in extreme cold and dry conditions (Jones et al. 2013). It seems that this lower selectivity is also a reason to allow large disjunct areas, such as the area of the bipolar alpine lichen *U. africana*.

In the present study, we report *U. africana* for the first time in the Arctic and, given the considerable latitudinal distance to the nearest known habitats, we suggest that long-distance dispersal by birds is the most likely mode of dispersal. Furthermore, we found particular extant species of migratory birds linking localities of *U. africana* in the alpine belt of the tropical mountains and the Chukchi sector of the Arctic. In the absence of fresh material from the Arctic and Malaysia, we are unable to use DNA sequence data to analyse the genetic origins of *U. africana* in those areas. Despite the inaccessibility of the regions, we need to obtain these data in future studies to generate a calibrated phylogeny of *U. africana*, to shed light on the origin, timing, and direction of migrations. The detection of extensive gene flow would indicate high connectivity between sites, whilst the detection of region-specific haplotypes would reveal population isolation and the molecular clock would suggest the timing of long-distance dispersal events.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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