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Calluna vulgaris and *Spiranthes amoena* in the Colchis mire flora: weeds or relicts?

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ABSTRACT. Recent botanical discoveries in the Colchis lowland of Western Georgia have renewed interest in the extensive *Sphagnum* peat bogs along the Black Sea coast. This area has long been recognized as an important refugium for thermophilous, Tertiary relict plants, but is also home to some plants typical of the boreal zone. In this paper, we present palynological and historical data that calls into question the idea that *Calluna vulgaris* (L.) Hull and *Spiranthes amoena* (Bieb.) Spreng., the Euro-Siberian elements recently discovered in the Colchis *Sphagnum* bogs, are adventive. We argue instead that they are relicts of late Pleistocene age that elsewhere in the Western Asia were pushed out by afforestation and sea-level rise during the early-mid Holocene.

KEY WORDS: *Sphagnum* bogs, pollen data, Quaternary, Colchis, Georgia

INTRODUCTION

The expansive peat bogs along the Black Sea coast of Western Georgia have been the subject of much recent scientific attention (Akhalkatsi et al. 2004, Akhalkatsi & Mosulishvili 2004, Connor et al. 2007, Denk et al. 2001, Joosten et al. 2003, Kaffke et al. 2000, 2002, Matchutadze 2004, Matchutadze & Skhiladze 2003). Surrounded by the largely arid and mountainous lands of Anatolia and the Caucasus, these peat bogs occupy a unique geographical situation with exceedingly high rainfall and a warm temperate climate. Peat accumulation rates in these ombrotrophic bogs are correspondingly rapid – as much as 4 mm *per annum* (Joosten et al. 2003).

Colchis, as the coastal lowland of Western Georgia has been known since ancient times, is an important refugium for Tertiary relict plants (Denk et al. 2001, Berg 1950, Kikvidze & Ohsawa 2001, Tumajanov 1971). The Colchic or Euxinian refugium, together with the Hyrcanian (Lenkoran and Talysh) refugium along the southern coast of the Caspian Sea, forms the most important component of the Transcaucasian refugium (Fig. 1), one of three major refugia in the Middle East (Röhrig 1991). Colchis is also one of the three major refugia of Tertiary relict taxa worldwide (Milne & Abbott 2002). The Colchic refugium is home to such relict taxa as *Pterocarya fraxinifolia* (Michx.) Kunth, *Zelkova carpinifolia* (Pall.) C. Koch and many others from the Tertiary and younger periods (Nakhutsrishvili 1999, Dolukhanov 1966, Walter 1974).

Some relict plants in Colchis nowadays have their main distributions in East Asia, the Mediterranean, the Balkans, and northern Eurasia. It is the group currently distributed through the last of these regions – the so-called boreal or Euro-Siberian elements – that is the focus of this paper. In recent years, two Euro-Siberian plant species *Calluna vulgaris*

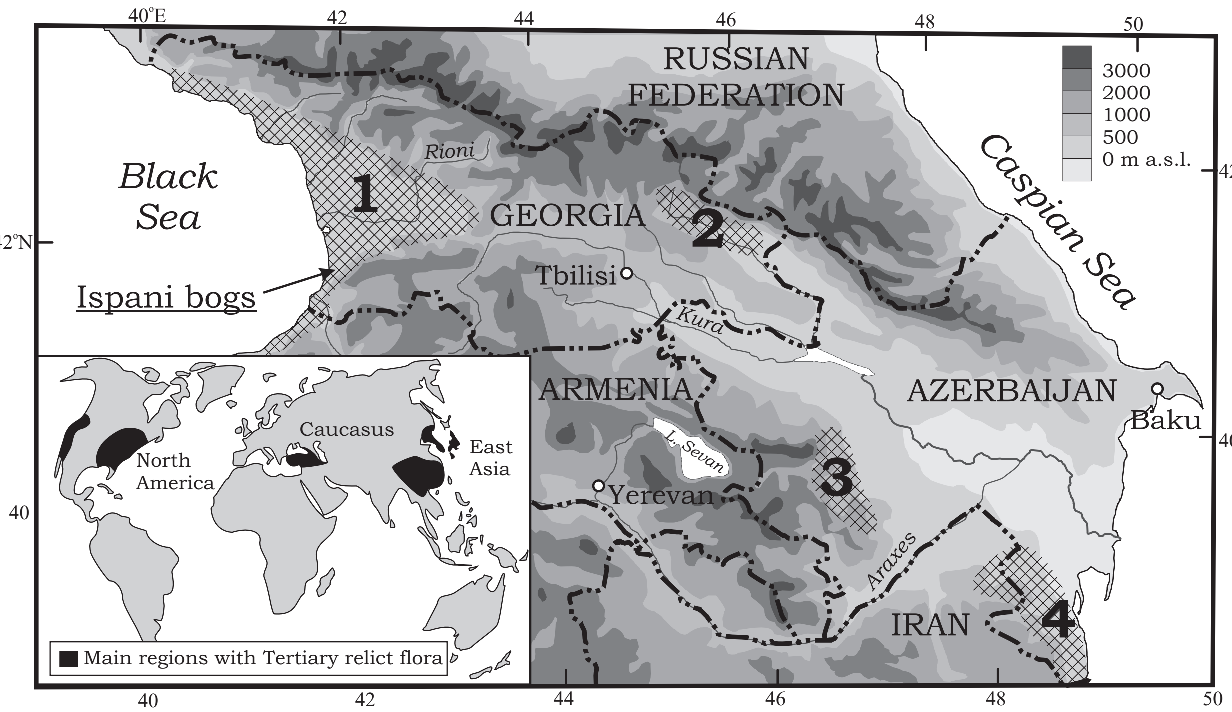

Fig. 1. Topographic map of the Caucasus region with location of the Ispani bogs. Cross-hatching indicates areas with important populations of Tertiary relict plants: **1** – Colchis; **2** – Alazani Valley; **3** – Nagorno-Karabakh; **4** – Lenkoran. Inset: worldwide distribution (after Milne & Abbott 2002)

(L.) Hull and *Spiranthes amoena* (Bieb.) Spreng. have been identified in Colchis for the first time. Here we examine current theories for their occurrence in the light of historical evidence and palynological data.

GEOGRAPHICAL SETTING

Colchis ("Kolkhida" in Russian, "Kolkheti" in Georgian) encompasses the vast alluvial lowlands of Western Georgia, bordered to the north by foothills of the Caucasus Mountains, by the Anticaucasus Mountains to the south, the Likhi Range to the East, and the eastern shore of the Black Sea to the west (Fig. 2). In an otherwise mountainous country, Colchis has a relatively muted relief and is crossed by a number of large rivers (Rioni, Enguri, Supsa, etc.).

The warm, humid climate of Colchis led Russian scholars to term this a "subtropical" region (Berg 1950). The climate is wet temperate, with coastal areas of southern Colchis receiving annual precipitation over 2000 mm (Fig. 2). Kobuleti, where the peat bogs described in this paper are located, receives 2365 mm of rain in an average year, has a mean temperature around 14°C and relatively few frosts (Davitaia & Seperteladze 2000). The climate is heavily influenced by westerly air streams from the Black Sea and can rightly be described as "oceanic" (Rübel 1914). This oceanic climate, perhaps more than any other factor, explains the persistence of Tertiary and other relict plants in Colchis.

The coastline of Colchis is characterized by swampy alluvial soils, coastal lagoons (the largest of which is Lake Palaeostomi) and a number of ombrotrophic peat bogs. The vegetation of Colchis has been heavily human-impacted over the past century, with extensive drainage works to allow agricultural use of formerly waterlogged soils and the establishment of tea and citrus plantations (Badenkov et al. 1990, Walter 1974). The remaining areas of natural vegetation are described in detail by Denk et al. (2001), and the following altitudinal zones can be distinguished (Ketskhoveli 1959):

0–50 m a.s.l. – *Sphagnum* peat bogs, and swamp forests dominated by *Alnus barbata* C.A. Mey;

50–200 m a.s.l. – Colchic liana forest on wet soils, with forests of *Fagus orientalis* Lipsky and *Carpinus caucasica* Grossh. and others in better-drained places;

200–500 m a.s.l. – Colchic forest with evergreen understorey (*Ruscus aculeatus* L.,

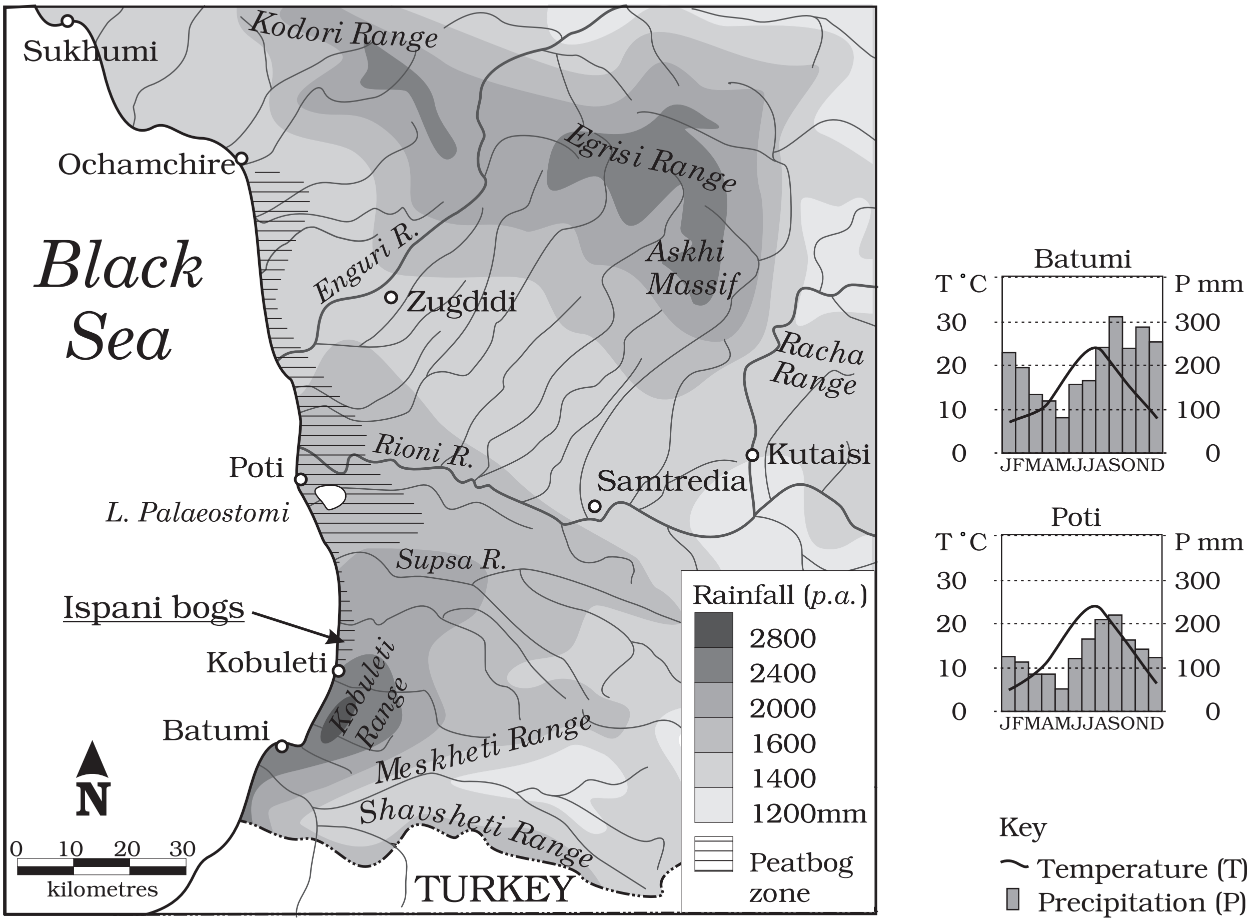

Fig. 2. Map of the Colchis lowland showing the distribution pattern of annual rainfall, zone of lowland peat bogs and surrounding mountain ranges. Seasonal climatic characteristics are given for the towns of Batumi and Poti (after Atlas of the Georgian SSR 1964)

Buxus colchica Pojark., *Laurocerasus officinalis* M. Roem., *Ilex colchica* Pojark., etc.).

The bog flora of Colchis is dominated by the following *Sphagnum* species: *S. papillosum* Lindb., *S. imbricatum* Hornsch. ex Russ., *S. palustre* L., and *S. rubellum* Wils. Other plant species of importance are listed in Table 1.

Table 1. Characteristic species of the bog flora of Colchis (Ketskhoveli 1959, Akhalkatsi et al. 2004, Joosten et al. 2003, nomenclature follows Czerepanov 1995). Euro-Siberian species are shown in **bold typeface**

Species	
Agrostis stolonifera L.	*Pteridium tauricum* V. Krecz.
Alnus barbata C.A. Mey.	*Pycreus colchicus* (C. Koch) Schischk.
Calluna vulgaris (L.) Hull	*Rhododendron luteum* Sweet
Carex lasiocarpa Ehrh.	*Rhododendron ponticum* L.
Drosera rotundifolia L.	***Rhynchospora alba*** (L.) Vahl
Frangula alnus Mill.	*Rhynchospora caucasica* Palla
Hibiscus ponticus Rupr.	*Scirpus colchicus* Kimeridze
Juncus acutus L.	*Smilax excelsa* L.
Juncus effusus L.	*Solidago turfosa* Woronow ex Grossh.
Lycopodiella inundata (L.) Holub	***Sphagnum imbricatum*** Hornsch. ex Russ.
Lycopus europaeus L.	***Sphagnum palustre*** L.
Lysimachia vulgaris L.	***Sphagnum papillosum*** Lindb.
Menyanthes trifoliata L.	***Sphagnum rubellum*** Wils.
Molinia litoralis Host	***Spiranthes amoena*** (Bieb.) Spreng.
Osmunda regalis L.	*Thelypteris palustris* Schott
Potentilla erecta (L.) Raeusch.	*Vaccinium arctostaphylos* L.

CALLUNA VULGARIS (L.) HULL AND *SPIRANTHES AMOENA* (BIEB.) SPRENG.

Two Euro-Siberian species have recently been discovered growing on a *Sphagnum* bog known as Ispani-II, near the town of Kobuleti in southern Colchis (Kaffke et al. 2002, Akhalkatsi et al. 2004). These are populations of *Spiranthes amoena* (Orchidaceae) and *Calluna vulgaris* (Ericaceae). Both plants are characteristic of the northern latitudes of Eurasia in the present day (Tutin et al. 1964, Beijerinck 1940).

Calluna vulgaris is distributed throughout Europe, with south-western outposts in Morocco and the Azores. It extends eastward to the Ural Mountains and western Siberia, and in the southeast to Thrace, northern Anatolia and the Carpathians (Browicz 1982, Beijerinck 1940). It was discovered on the Ispani bogs in the year 2000, covering an area of 0.2 ha (Kaffke et al. 2002).

Spiranthes amoena occurs over a wide area of northern Eurasia: from the Carpathians and Urals eastward through Siberia, Kazakhstan and Mongolia to the Far East where it merges with *Spiranthes sinensis* (Pers.) Ames., a possibly synonymous species found in East Asia and Oceania (Akhalkatsi et al. 2004). A 2-ha area of population of *S. amoena* was discovered on the Ispani bogs in 2001 (Akhalkatsi et al. 2004).

The occurrence of *Calluna vulgaris* and *Spiranthes amoena* in Western Caucasus was attributed, in the case of *Spiranthes*, to its escape from the Batumi Botanical Gardens and subsequent proliferation (Kaffke et al. 2002, cf. Akhalkatsi et al. 2004), and, in the case of *Calluna*, to its accidental introduction by Russian soil scientists whose clothing or equipment was contaminated by *Calluna* seeds when they visited the Ispani mires in the 1930s (Kaffke et al. 2002).

POLLEN EVIDENCE

Kaffke et al. (2002) justified this conclusion with pollen data from a 110-cm-deep peat core taken from a spot on the Ispani-II bog where *Calluna vulgaris* plants were growing *in situ*. *Calluna* pollen appears at a depth of 69 cm in the sediments. Initially its appearance was dated to 1900 AD, by interpolating a radiocarbon date (1021±33 ^{14}C yr B.P.) taken from a depth of 4 metres in a different part of the mire and by using pollen accumulation as a proxy for sedimentation rates. This date was revised to 1920–1930 AD to account for a recent reduction in forest cover and hence pollen influx (Kaffke et al. 2002). It is difficult to accept this revised date, since the method used to calibrate pollen influx and forest cover is not described.

Perhaps it is more reliable to use *Ambrosia*-type pollen (an introduced taxon) as a biostratigraphic marker. *Ambrosia artemisifolia* plants were introduced to Colchis from North America in the 1930s (Dr. Zurab Manvelidze, Batumi Botanical Garden, pers. comm., 2005). *Ambrosia artemisifolia* is an annual plant that produces abundant pollen, so its appearance in pollen records should occur soon after its introduction. The *Ambrosia* pollen curve presented by Kaffke et al. (2002) begins to rise from a depth of 19 cm, which is 50 cm above the *Calluna* pollen. This suggests that *Calluna* was present on the Ispani-II bog prior to the 1930s.

A single grain of *Calluna* pollen was identified in a new pollen record from a different location on the same mire at a depth of 275 cm (Fig. 3). Mirroring the previous pollen record, introduced *Ambrosia* increases in the upper 24 cm, as does *Cryptomeria* pollen. *Cryptomeria japonica* L.D. Don is an introduction from East Asia, grown in the Batumi Botanical Garden from 1939 and thereafter widely planted throughout the regions of Ajara and Guria (Sharadze 1987).

During the 1920s and 1930s, peat was extracted from the southern part of the Ispani bogs on a large scale (Joosten et al. 2003), and the entire Colchis lowland was subject to extensive deforestation, drainage and reclamation projects to increase productivity for mechanised, collectivised agriculture (Ketskhoveli 1959, Badenkov et al. 1990). Palynologically, these human impacts, along with the introduction of *Cryptomeria* and *Ambrosia* (both abundant pollen producers), would be expected to manifest in the pollen record at much the same time. *Calluna* pollen, however, appears in the pollen records earlier than the increase in *Ambrosia*, *Cryptomeria*, *Urtica,* and *Pinus*, the appearance of *Zea mays* or the decline in *Carpinus*, *Fagus* and *Alnus* (Fig. 3), all of which are most probably associated with

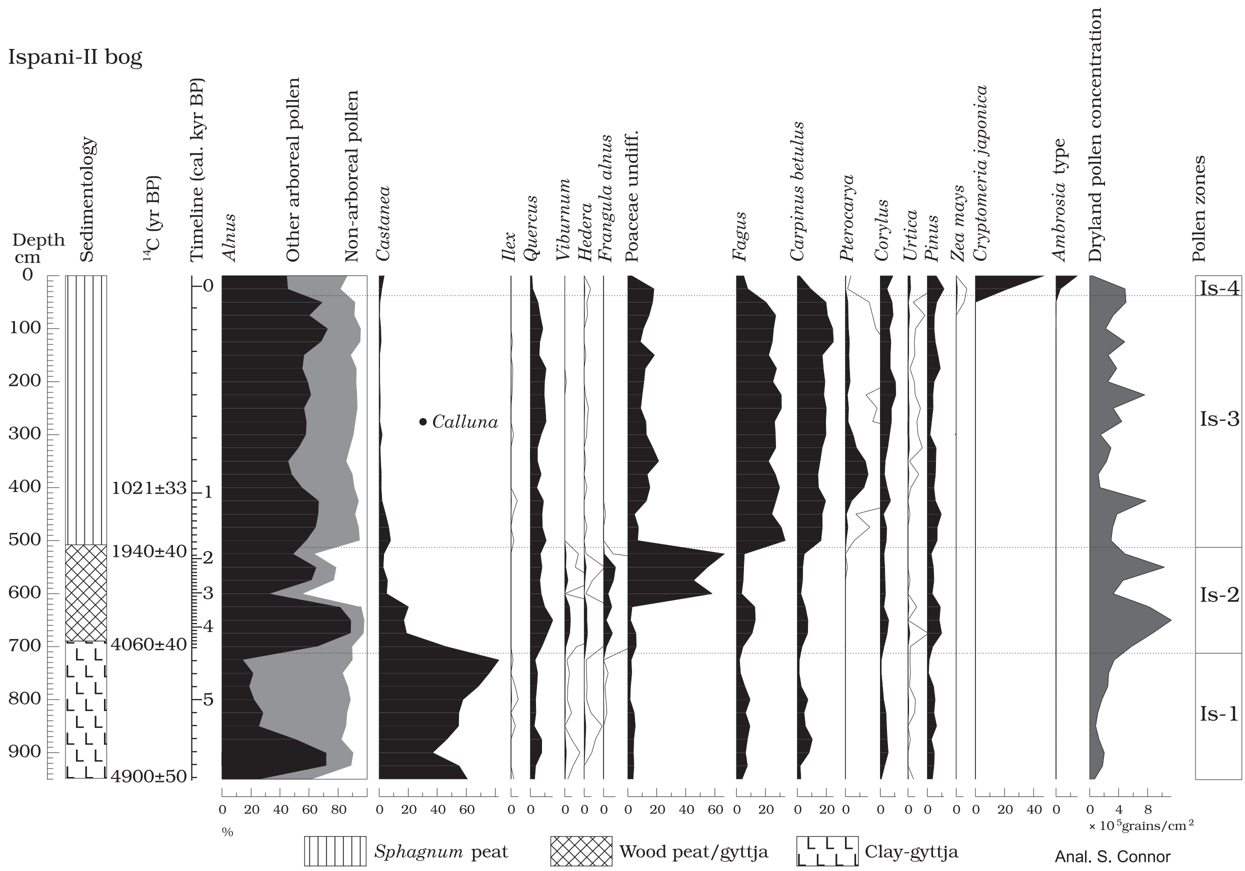

Fig. 3. Summarized pollen diagram from the Ispani-II bog, showing the occurrence of *Calluna* pollen in relation to taxa introduced in the 1930s (*Ambrosia*-type and *Cryptomeria*) and radiocarbon dates. Date of 1021±33 ^{14}C yr BP from Joosten et al. (2003). See Connor et al. (2007) for the complete diagram

intensive agricultural development of the Colchis lowland beginning in the early-mid 20th century.

Whilst it is conceivable that an increase in anthropogenic indicators and decline of forest taxa accompanied post-Soviet land-use changes (Kaffke et al. 2002), this is unlikely to be the event recorded in the pollen diagram (Connor et al. 2007). *Cryptomeria* plantations were established in Colchis decades before 1991 AD, and coppicing and clearing in the post-Soviet period was minor compared to the large-scale deforestation that took place in the 1920s and 1930s (Ketskhoveli 1959).

The earliest occurrence of *Calluna* in each of the Ispani pollen records therefore appears to pre-date the introduction of *Ambrosia* and *Cryptomeria* to Western Georgia in the 1930s. An even earlier, mid-Holocene, occurrence of *Calluna* pollen was found in the well-dated sediments of Didajaris Lake in the mountains of Ajara, some 60 km east of the Ispani bogs (J.F.N. van Leeuwen, Bern University, unpublished data). Hence the possibility of relict status must be entertained.

Palynological methods are not entirely satisfactory when attempting to determine when *Calluna vulgaris* and *Spiranthes amoena* established in Colchis. *Calluna vulgaris* has relatively poorly dispersed pollen, which is only likely to be found in peat accumulated near plants growing *in situ* (Kaffke et al. 2002). The pollen tetrads of *Spiranthes* tend to disintegrate on maturation (Yueng 1987), so they are very unlikely to be identified by palynologists, and the pollen itself is primarily dispersed by insects. So, while the relative dating issues outlined above could be resolved by further radiometric dating, this can, at best, only tell us when the populations established in a precise location, not their history in the Ispani bogs nor Colchis as a whole.

SEED DISPERSAL MECHANISMS

If Russian peat scientists did not introduce *Calluna* during their excursions during the 1930s, then alternative modes of introduction ought to be considered. The notion (cf. Kaffke et al. 2002) that *Calluna vulgaris* diaspores could be spread to the Ispani bogs by migratory birds is doubtful: the seeds of *Calluna* are unsuitable for epizoochorous dispersal, lacking the requisite burrs, spines or awns that characterize diaspores of long-distance-dispersed adventive plants (van der Pijl 1969). If the seeds were dispersed by birds, we might ask why they established only in the Ispani bogs, which are at the southernmost limits of the Colchis wetland system and much smaller than the very extensive Nabada and Imnati wetlands that surround Lake Palaeostomi on the central Colchis plain (Fig. 2; Akhalkatsi et al. 2004).

Like *Calluna*, the tiny seeds of the Orchidaceae are produced in great numbers for dispersal by wind (Willson 1983). The possibility of wind transport can be ruled out owing to the huge distances involved. The likelihood of such tiny seeds surviving an avian migration from Siberia or the Far East is somewhat remote, and because the germination of *Spiranthes amoena* seeds is reliant on symbiosis with specific mycorrhizal fungi (Masuhara & Katsuya 1994), the chance of these seeds developing into a viable population of adult plants is small. Again, if such a journey were possible, mires have been continuously accumulating along the 100 kilometres of Colchis coastline for 6000–7000 years (Bogolyubova 1990, Neishtadt et al. 1965) and it is surprising to find only two populations confined to the Ispani-I and Ispani-II bogs, containing 500–1000 individual plants and covering several hectares. The possibility of these plants having been inadvertently introduced from the Batumi Botanical Garden (Kaffke et al. 2002) is complicated by the fact that there are no records of the orchid ever having been planted there (Akhalkatsi et al. 2004).

BEHAVIOUR OF ADVENTIVE PLANTS

One overlooked aspect of these recently discovered populations of *Calluna* and *Spiranthes* is that they appear not to be expanding into new habitats, as one would expect when an exotic, adventive species colonises new territory. *Calluna vulgaris* is obviously capable of rapid spread, as its postglacial history in northern Europe indicates (Godwin 1975). There are plentiful examples of normal adventive plants, quickly spreading along the Black Sea coast, such as *Baccharis halimifolia* L., *Bothriochloa virginicus* L., *Oplismenus undulatifolius* (Ard.) Beauv., *Paspalum dilatatum* Poir., and *Ambrosia artemisifolia* L. (Dmitrieva 1990, Sokhadze 1990). These are widespread and have completely displaced the indigenous vegetation in some places.

It is interesting to note by way of example that *Sequoia*, a species of which was prevalent in Colchis during the Pliocene before becoming extinct during repeated Pleistocene glaciations (Shatilova & Ramishvili 1990), was introduced to parts of Western Georgia in 1934 and is now reproducing and expanding without human intervention (Kvavadze 1988).

Calluna and *Spiranthes* display no invasive tendencies they are confined to only small, isolated populations on the Ispani bogs (Akhalkatsi et al. 2004, Kaffke et al. 2002). This stenotopic behaviour is characteristic of relict species due to the decline of their optimal ecological conditions. Because of this, *Spiranthes amoena* is considered critically endangered in Georgia (Akhalkatsi et al. 2004).

OTHER EURO-SIBERIAN ELEMENTS

Spiranthes amoena and *Calluna vulgaris* are not the only "boreal" elements found in the Colchis bogs. Others include *Menyanthes trifoliata*, *Drosera rotundifolia*, *Rynchospora alba*, *Carex lasiocarpa*, and the moss species that comprise the bog vegetation itself: *Sphagnum imbricatum*, *S. papillosum*, *S. palustre*, and *S. rubellum* (Table 1; Ketskhoveli 1959). As early as 1936, it was noted that, for the Caucasus region, "the *Sphagnum* bogs along the Batumi coast have an appearance that is quite unusual. They are of the same type as those much further north, having all the attributes of northern bogs" (Dokturovsky 1936, p. 184).

In pre-Quaternary times, *Sphagnum* bogs existed in Colchis and were of the same type as Atlantic *Sphagnum* bogs (Dokturovsky 1936, Sosnovsky 1943, Grossgeim 1948, Ketskhoveli 1959, Kolakovsky 1961, Shatilova et al. 2004). Later, during the Quaternary, the flora of the Colchis mires was enriched with a number of "boreal" taxa (Nakhutsrishvili 1999). The occurrence of *Menyanthes*, *Drosera*, *Rynchospora*, *Carex* and various northern-latitude *Sphagnum* species can therefore be ascribed to the southward migration of Euro-Siberian flora during the Pleistocene glaciations, rather than to adventive introduction, because these species together constitute elements of a complete Euro-Siberian mire ecosystem. Is it possible that the two recently discovered species in Colchis are also relicts of that time? We suggest that the Colchis bog flora represents the most southerly distribution of the boreal mire flora, which probably survives here only because of the exceedingly high rainfall and constant humidity experienced by the Black Sea coast of Georgia.

TOPOGRAPHY AND REFUGIA

The Ispani bogs are set apart from the extensive peat-lands of central Colchis by their greater number of relict species. This raises the question of what environmental factors contributed to the preservation of these species in southern Colchis. We consider that topography played a significant part. The Ispani bogs occupy a narrow coastal strip between the Kobuleti Range and the Black Sea (Fig. 2). The bogs of central Colchis around Poti occupy a flat coastal plain built of Quaternary alluvial sediments. During the Pleistocene low sea level stands, when the Black Sea existed as a lake and the climate was cold and arid, deep gorges on the westward side of mountains in southern Colchis gave protection to thermophilous and hygrophilous taxa (Kolakovsky 1961). Orographic rain provided consistent moisture, and deep snow cover in winter insulated these gorges from the cold desiccating winds that are thought to have wiped out Tertiary relicts on more exposed, flat terrain (Kolakovsky 1961).

The gorges of southern Colchis (Ajara) are floristically very rich, combining mesophytic elements of the Mediterranean, Hyrcanian, Euro-Siberian, East Asian and Colchic/Euxine floras (Nakhutsrishvili 1999). Colchic forests are unique for their relict taxa, evergreen understorey and high representation of lianas (Rübel 1914, Nakhutsrishvili 1999). The well watered, steep mountain gorges near the Ispani bogs were almost certainly the principal refugium for many plants during the Pleistocene glaciations, which may explain the occurrence of relict taxa in the Ispani bogs that are lacking in the bog flora of central Colchis.

DISTRIBUTION PATTERNS

When the location of the "new" *Calluna vulgaris* population is compared with its existing distribution in northern Anatolia and the Carpathians (Fig. 4), it seems plausible that the Colchis population is merely an extension of this distribution, rather than an adventive occurrence.

Some 170 years ago, in 1837, Karl Koch

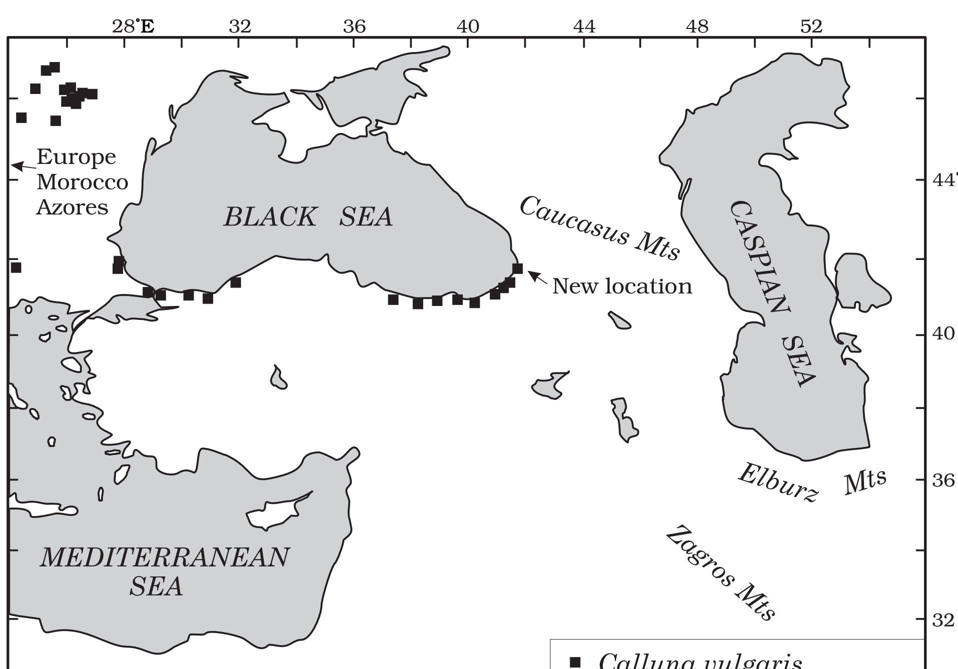

Fig. 4. Distribution of *Calluna vulgaris* in the Middle East (after Browicz 1982), showing the location of the new Georgian population

first described *Calluna vulgaris* growing in Colchic vegetation at the mouth of the Of river, between the Turkish towns of Trabzon and Rize, approximately 150 kilometres southwest of the Ispani bogs (Table 2; Beijerinck 1940, Edmondson & Lack 1977). This population was reported again in 1866 and 1907 (Beijerinck 1940, Davis 1965). The occurrence of *Calluna vulgaris* plants in Georgia was reported in the 1930s, from the headwater bogs of the Qvirila river (Bush 1932). There is no evidence to suggest that the vectors invoked by Kaffke et al. (2002) for the occurrence of *Calluna* in Colchis (i.e. migratory birds, Soviet trade movements, Russian peat scientists) were responsible for the taxon's spread along the entire southern coast of the Black Sea, especially as the Turkish *Calluna* populations were alive at least 80 years before Russian peat scientists first trudged their muddy boots through the *Sphagnum* bogs of Colchis.

Table 2. *Calluna* occurrences in W Georgia and NE Anatolia from botanical and palynological sources. Dates marked with an asterisk (*) are interpolated from calibrated radiocarbon ages and are approximations only

Year	Location	Source
1932 AD	Headwaters of Qvirila r., W Georgia	Bush (1932)
1907 AD	Mouth of Of r., Lazistan, NE Turkey	Handel-Mazetti: see Beijerinck (1940)
1900 AD*	Ispani II bog, Black Sea coast, SW Georgia	Kaffke et al. (2002) pollen data
1866 AD	Mouth of Of r., Lazistan, NE Turkey	Balanza: see Beijerinck (1940)
1837 AD	Mouth of Of r., Lazistan, NE Turkey	Koch: see Beijerinck (1940)
1300 AD*	Ispani II bog, Black Sea coast, SW Georgia	This paper, pollen data
3050 BC*	Didajaris Lake, 1850 m elevation, S Georgia	J. van Leeuwen, unpubl. pollen data

It is generally accepted that most of the Colchis was densely forested throughout the Holocene (Neishtadt 1957, Dzhanelidze 1980, Margalitadze 1995). The climate here is so moist and tree growth so rapid that abandoned cornfields have been known to vanish beneath 6-metre-high thickets of *Alnus barbata* and *Pterocarya fraxinifolia* within two years (Berg 1950). Light-demanding plants unable to adapt to understorey shade (e.g. *Hippophaë rhamnoides* L.) are therefore confined to the narrow coastal fringe where unstable sand dunes or boggy soils prevent the establishment of a dense forest canopy. It may be that *Calluna vulgaris* and *Spiranthes amoena* were more widely distributed during less forested periods or times when the coastline was less stable than it is presently.

The principal habitat of *Calluna vulgaris* today is in the treeless heathlands and peatlands of the northern latitudes. In contrast, *Calluna* populations along the Black Sea coast of Turkey are found amongst woodland and scrub vegetation (Davis 1965, Beijerinck 1940). The Black Sea coast's dense Colchic liana forests presently provide poor habitat for what is characteristically a light-demanding shrub (Browicz 1982).

CONCLUSION

The evidence presented in this paper calls into question the status of *Calluna vulgaris* as an adventive plant in the mire flora of Colchis. Historical evidence demonstrates that *Calluna* grew in Colchic vegetation well before the 20th century and pollen data indicate its presence at various times during the mid-late Holocene. A lack of palynological data from the early Holocene and late Pleistocene prevents an assessment of the taxon's earlier history.

While the biogeographical problems raised in this paper are not likely to be resolved by palaeoecological methods alone, they may be illuminated by comparing the molecular profiles of the plants in question. If, for instance, the various *Calluna vulgaris* populations along the southern Black Sea littoral share closer genetic links with each other than with populations in the Mediterranean and the boreal zone, one might conclude that those plants constitute a circum-Euxine refugium, established during the cooler, less wooded conditions of the late Pleistocene.

Until such work is undertaken, we argue that while there is a possibility that the many Euro-Siberian plants found in Colchis arrived separately and adventively, there are sound palaeoecological and biogeographical reasons to believe that Colchis retains relicts of the

Euro-Siberian mire flora by virtue of a unique combination of high rainfall and steep topography.

Elsewhere in Western Asia many of these wetland plants were extirpated from suitable habitats by early-mid Holocene afforestation and sea-level rise. Hence it is imperative that these bogs, already marginalized and now threatened by drainage works, overgrazing and urbanisation, be carefully monitored and conserved as a rare wetland ecosystem in a largely arid region.

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