Reviewed research article

Upper Tertiary non-marine environments and climatic changes in Iceland

Friðgeir Grímsson[1,2] and Leifur A. Símonarson[1]
[1]*Institute of Earth Sciences, University of Iceland, Askja, Sturlugata 7, 101 Reykjavík*
[2] *Icelandic Institute of Natural History, Hlemmur 3, 105 Reykjavík*
fossil@hi.is; leifuras@raunvis.hi.is

Abstract — *Palaeontological research on the Miocene and Pliocene floras and faunas of Iceland date back to the 1770's. At that time, plant fossils from Iceland were considered belonging to a single flora, and in the early 20th century scientist considered this flora of Eocene age. During the past few decades systematic palaeontology, palaeoclimatology, stratigraphy, and palaeogeography have been linked to results from isotopic (K/Ar and Ar/Ar) absolute age determinations and palaeomagnetic measurements of Cainozoic lavas in Iceland. As a result, numerous fossil floras and a few faunas identified from terrestrial sediments in Iceland are now known to give a contiguous record dating back 15 Ma. The oldest floras are therefore Middle Miocene in age. Younger floras are quite different from the older ones and their composition changed as the Miocene came to an end. Gradual cooling that occurred on Iceland since 12 Ma, when the climate was mild with no dry season and warm summers, and continuous isolation of Iceland, in the northern North Atlantic, had its affect on the Icelandic flora. Thermophilous plants soon became extinct and more cold tolerant species became prominent.*

INTRODUCTION

The fossil record of Iceland extends back as far as its oldest rocks, which have been radiometrically dated to about 15 Ma (McDougall *et al*., 1984; Hardarson *et al*., 1997). The Icelandic lava pile formed almost exclusively above sea level and as a result the fossil bearing strata are primarily of terrestrial origin. A number of sedimentary formations containing identifiable plant remains occur interstratified with the lavas (Figure 1). Studies of their fossil floras were initiated more than a hundred years ago and a Miocene age was correctly assigned to the oldest of them (Heer 1868). This was later rejected in favour of an Eocene age and that view persisted into the 1960's (see Kristjánsson, 1993). Radiometric dating of the lavas, which started in the mid-1960's, verified that the floras could be no older than Miocene, as originally proposed by Heer (1868). The global cooling that has occurred on Earth since the Middle Miocene is well documented in the record of fossil floras in Iceland, owing to the regular spacing of plantbearing sedimentary formations within the lava pile (Figure 2). Unfortunately, well preserved remains of terrestrial faunal assemblages are rarely found in these formations.

Iceland is the only landmass in the northern North Atlantic that has a fairly continuous fossil record from the early Middle Miocene to the present. The geographical position of Iceland, between Greenland and continental Northwest Europe, and its rich fossil record makes it an interesting place to study possible transcontinental migration of plants and animals between North America/Greenland and Europe/Asia during the Late Cainozoic and to interpret and reconstruct palaeoclimate and palaeoenvironment in the northern North Atlantic based on terrestrial proxies.

PALAEOENVIRONMENTS

The geology of Iceland is fairly well known (see Saemundsson, 1979; Steinthórsson and Thorarinsson, 1997; Thordarson and Höskuldsson, 2002). At present, extensional forces that are driven by up-flowing magma along the Mid-Atlantic Ridge cause many of the geological features of the island (Steinþórsson, 1981). The volcanic and tectonic environments of present-day Iceland have been the same for millions of years, or since the mantle plume became positioned under proto-Iceland, between Greenland and Scandinavia (Vink, 1984).

During the Miocene and Pliocene Iceland was, as it is now, characterized by volcanic systems with large central volcanoes and surrounding fissure swarms and crater rows (Walker, 1959, 1964; Hald *et al.*, 1971). Eruptions were frequent (Saemundsson, 1979; McDougall *et al.*, 1984, 1987) and of various types as evident by various sorts of igneous rocks in the geological formations of the island (Walker, 1959).

Even though modern day Iceland is characterized by U-shaped fjord landscape this was not so during the Miocene and Pliocene. The fjord landscape of north-western and eastern Iceland (Figure 3A), was formed by the glaciers only during the last ice age, and the hyaloclastite (palagonite) mountains and ridges along the active rift zone crossing the island were also formed only during the last ice age (Pjetursson, 1901) and date back no further than 3 Ma (Geirsdóttir and Eiríksson, 1994).

Sedimentary rocks in the Tertiary formations of Iceland give critical information on various environments during the Miocene and Pliocene. Sediments of volcanic origin, lake, river and lagoon sediments, as well as various other types suggest diverse environments and changing landscape (Walker, 1959; Friedrich, 1966; Saemundsson, 1979; Roaldset, 1983; Grímsson, 2002; Grímsson, 2007a; Grímsson, *et al.*, 2007).

As evident from the geological record and based on volcanic products and sedimentary rocks one can visualize the Icelandic Miocene and Pliocene environments as following. Were ocean and land met there were long and sandy beaches and steep cliffs, and bay-mouth bars fronting bays forming lagoons. From the shoreline, vast lowlands with meandering rivers and streams, oxbow lakes, marshlands, floodplains and terraces, stretched towards the highlands. Volcanoes with an altitudinal range up to 2000 m (stratovolcanoes) marked the landscapes, with smaller shield volcanoes, spatter ring craters, scoria cones, cinder craters, explosion craters (maars), tuff rings, tuff cones, and calderas. Rivers and streams eroded canyons and valleys. V-shaped valleys, gorges, ravines, gullies, and steep canyons cut into the highland and high-lying valleys that were surrounded by volcanic mountains. Lakes were numerous and of various types, and formed, as some of the present Icelandic lakes, by volcanic activity or extensional rift forces. Large lakes could have been present in rift valleys, calderas, and following the closure of a lava flow at the mouth of a valley. Other lakes could have been present in small explosive craters reaching below groundwater level.

These environments were full of life as evident from the fossil record. Vegetation thrived from the lowland to highlands (Grímsson *et al.*, 2007) and freshwater animals (Friedrich, 1966; Friedrich *et al.*, 1972; Sigurðsson, 1975) occupied lakes and streams. Insects were common in various environments (Friedrich *et al.*, 1972; Heie and Friedrich, 1971) and small terrestrial mammals, herbivores, were grazing in the undergrowth (Símonarson, 1990).

THE MIOCENE–PLIOCENE SEDIMENTARY ROCKS

Upper Tertiary sedimentary rocks in Iceland are quite variable. The most prominent are of volcanic origin, ranging from thin ash layers (very fine tuff) to thick pyroclastic formations and ignimbrites. The grain size ranges from finest ash and lapilli tephra to large blocks and bombs (fine tuff, lapilli tuff, and volcanic breccias). The thickness of these sedimentary rocks can easily change over short distances, and the difference in grain size from one outcrop to the other is often quite substantial. Most of the ash layers, tephra, scoria beds, plinian pumice deposits, various pyroclastic units, and phreatoplinian deposits have undergone different stages of geothermal alteration due to

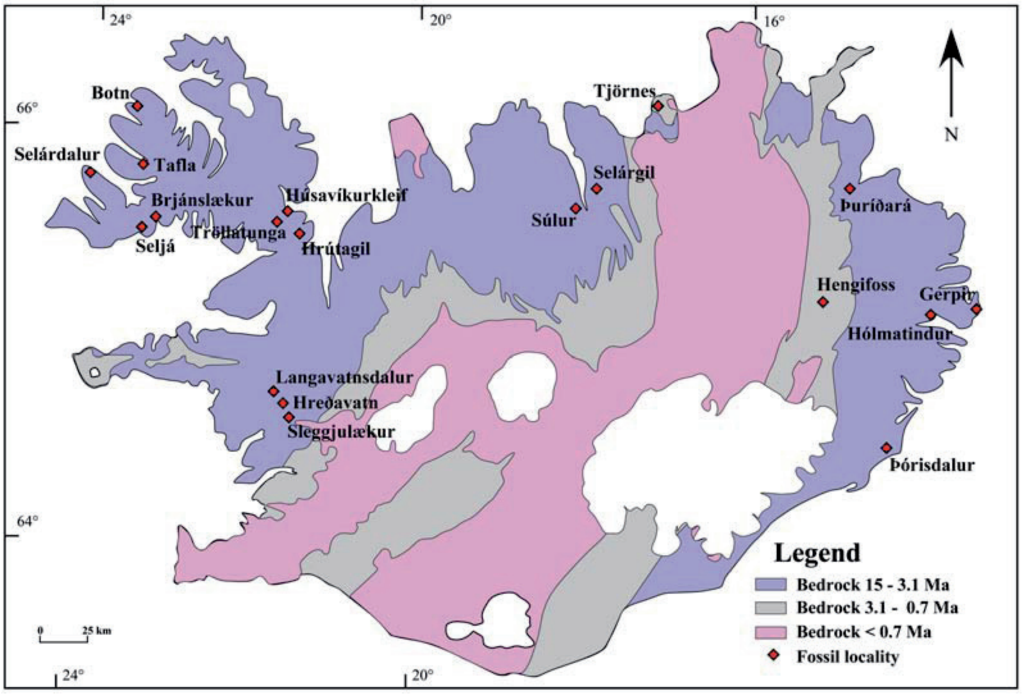

Figure 1. Geological map of Iceland with localities mentioned in the text (modified from Jóhannesson and Sæmundsson, 1989). – *Jarðfræðikort af Íslandi með fundarstöðum steingervinga sem nefndir eru í texta (byggt á korti Hauks Jóhannessonar og Kristjáns Sæmundssonar, 1989).*

loading and burial (Roaldset, 1983). The uppermost parts of sedimentary units have often been subjected to thermal metamorphism by overlying lava. All Tertiary sedimentary units have subsequently been subjected to burial diagenesis and low-grade metamorphism to zeolite facies (Roaldset, 1983). Loose particles have therefore become compact, cemented and lithified, forming hard glassy sedimentary rock.

Clastic sedimentary rocks in the Miocene–Pliocene strata are also quite variable with different types of clays, siltstones, sandstones and conglomerates. These sedimentary rocks show a diverse origin, having accumulated in lagoons, lakes, river channels, alluvial fans, deltas, on flood plains, in marshlands and swamps or other landforms (Grímsson, 2002, 2007a; Grímsson *et al.*, 2007). Relatively thin palaeosoils and aeolian silt- and sandstones of reddish colour are also prominent; they are frequently found separating two successive lava flows (Figure 3B). The red colour of some sedimentary units is partly believed to be the result of surface weathering in a warm and moist Miocene climate (Kristjánsson, 1973). Lacustrine sedimentary rocks are often present, usually having rather limited distribution but considerable thickness. The lacustrine rocks typically consist of thin-bedded shales, mudstones and siltstones interfingered with turbidites (Figure 3D) and overlain by coarser deltaic deposits of sandstone and conglomerate (Grímsson, 2007a). Fluvial sediments reflecting river channels and flood plains occur as large lenses of sandstone and conglomerate with surrounding thin-bedded shales that reappear and interfinger with coarser sediments. Delta marshland and swamp deposits are often found as various types of fine- to coarsely-grained, organic rich and dark coloured sedimentary rock (Grímsson, 2007a). These units are rich in plant remains (detritus) and are accompanied by numerous lignites or coal beds *(Icelandic: surtarbrandur)* (see Figure 3C), especially in the Miocene strata (Bárðarson, 1918). Other types of organic sedimentary rocks are not as common, with the notable exception of diatomite, made up of diatom silica shells that accumulated in a freshwater environment (Friedrich, 1968). The resulting sedimentary layer is yellow to whitish in colour and of low density (Figure 3D).

The present appearance and composition of the sedimentary rock types have resulted from a single or several secondary processes such as palagonitization and devitrification, weathering, thermal metamorphism (metasomatism), diagenesis, and regional burial metamorphism (Roaldset, 1983).

FOSSIL BIOTA

Remains of organisms from the Miocene and Pliocene in Iceland are found both in sedimentary and igneous rocks (Friedrich, 1968). To date, numerous plant fossils of angiosperms (Figure 3E), gymnosperms, mosses, club mosses, ferns and horsetails have been recorded. Plant parts that have been found include, among others: stems, branches, shoots, roots, leaves (Figure 3E), needles, fruits, capsules, catkins, cones, scales, samaras, seeds, rhizomes, fronds, pinnae, pollen, spores, and cuticles.

Fossils of terrestrial or freshwater animals from the Miocene and Pliocene of Iceland are rare. Insect remains (beetles) have been recorded from Brjánslækur (12 Ma) and in sedimentary rocks at Tröllа-

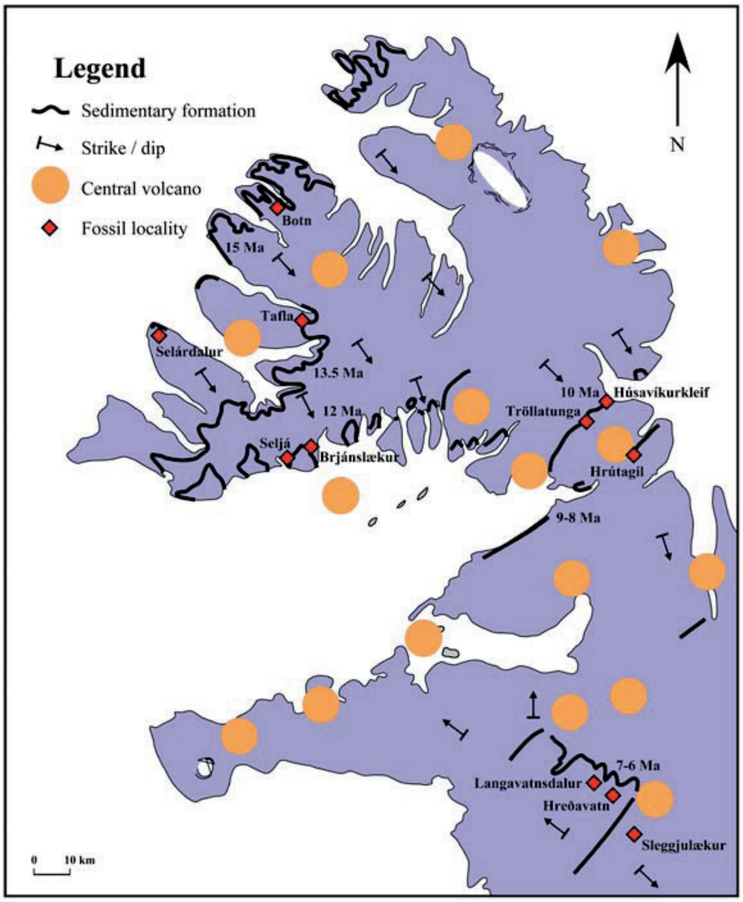

Figure 2. Map of Northwest Iceland showing the age of sedimentary formations, fossil localities, and extinct central volcanoes (modified from Jóhannesson and Sæmundsson, 1989; 1998). – *Kort af Vestfjörðum er sýnir aldur setlagamyndana, fundarstaði steingervinga og útkulnaðar megineldstöðvar (byggt á kortum Hauks Jóhannessonar og Kristjáns Sæmundssonar, 1989 og 1998).*

Figure 3. A) Typical fjord landscape in Northwest Iceland. B) Red intrabasaltic sediments with white tephra layers in Northwest Iceland, 15 Ma. C) Lignite (surtarbrandur) in Húsavíkurkleif, 10 Ma. D) Diatom-rich lake sediments in Surtarbrandsgil, Brjánslækur, 12 Ma. E) *Fagus friedrichii* Grímsson & Denk, from Selárdalur, 15 Ma. Scale bar 3 cm. F) Bones from a small deer, Þuríðará in Vopnafjörður, 3.5–3.0 Ma. Scale bar 2 cm. G) Trace fossils, repichnia, Þórisdalur, 6–5 Ma. Scale bar 2 cm. (Photos A and C-G from Friðgeir Grímsson, 2007; B: from Þorleifur Einarsson, 1974). – *A) Landslag á Vestfjörðum. B) Rautt setlag með ljósum gjóskulögum á milli hraunlaga á Vestfjörðum, 15 millj. ára. C) Surtarbrandur í Húsavíkurkleif, 10 millj. ára. D) Kísilríkt stöðuvatnaset í Surtarbrandsgili hjá Brjánslæk. E) Arnarbeyki frá Selárdal, 15 millj. ára. Mælikvarði er 3 cm. F) Bein úr litlu dýri af hjartarætt frá Þuríðará í Vopnafirði, 3,5–3,0 millj. ára. Mælikvarði er 2 cm. G) Skriðför í siltsteini frá Þórisdal í Lóni, 6–5 millj. ára. Mælikvarði er 2 cm. (Myndir A og C-G tók Friðgeir Grímsson, 2007, en mynd B tók Þorleifur Einarsson, 1974).*

tunga in Steingrímsfjörður deposited at 10 Ma (Figure 4). The best preserved insect remains were found at Hrútagil in Mókollsdalur, Northwest Iceland (Figures 1 and 2), in sedimentary rocks dated to 9–8 Ma (Heie and Friedrich, 1971; Friedrich *et al.*, 1972, Akhmetiev *et al.*, 1978). The occurrence of the aphid *Longistigma caryae* Harris (giant bark aphid) is interesting as this species is presently confined to North America. The North American-Icelandic aphid is most closely related to *L. liquidambara* Takahasi from Taiwan (Heie and Friedrich, 1971). This relation suggest a much wider circumpolar distribution of large aphids during the Miocene than at present. Several remains of flies, belonging especially to Bibionidae (marsh flies), have been found in the sedimentary rocks in Mókollsdalur. Insect remains have also been found in Langavatnsdalur and around Hreðavatn, West Iceland (Figures 1 and 2), in sedimentary rocks dated to 7–6 Ma (Figure 4).

Spicules of fresh water sponges (*Spongilla* cf. *fragilis*) have been recorded from Surtarbrandsgil at Brjánslækur in sedimentary rocks dated to about 12 Ma (Friedrich, 1966). Remains of water fleas (*Daphnia* sp., belonging to Cladocera) have been found at Hrútagil in Mókollsdalur. Freshwater pulmonate gastropods have been collected from Mount Súlur close to Akureyri (Figure 1) in sedimentary rocks slightly younger than 8 Ma (Margrét Hallsdóttir *pers. comm.*, 2007), as well as a few schizodont bivalves most likely belonging to Unionidae in about 5.5 Ma old sedimentary rocks in Selárgil in Fnjóskadalur (Figures 1 and 4), North Iceland (Sigurðsson, 1975).

Trace fossils, mainly foodichnia, domichnia, repichnia, and pascichnia, reflecting the activity of invertebrates, are quite frequently found in Icelandic Miocene and Pliocene freshwater sedimentary rocks, such as those around Hreðavatn and at Þórisdalur (6–5 Ma) in Southeast Iceland (Figure 3G). They are often found even when there are no body fossils (Vilhjálmsson and Símonarson, 1987; Grímsson, 2002). Trace fossils such as leaf mines, galls, pierce holes, and various traces left by a range of insects are also found in fossil plants remains (F. Grímsson, *unpub. material*).

Terrestrial vertebrate fossils are extremely rare in Iceland (Figure 3F). So far only fragmentary shoulder bones, scapula and other bone parts belonging to a small deer have been found (Símonarson, 1990). The bones were found in the Burstarfell Formation at Þuríðará in Vopnafjörður (Figures 1 and 4) in red interbasaltic sandstone of Pliocene age, 3.5–3 Ma. The animal was probably a descendant of the terrestrial vertebrate fauna that found itself isolated on proto-Iceland when it became an island in the Late Oligocene or Early to Middle Miocene.

MIOCENE–PLIOCENE VEGETATION

The oldest floras known from Iceland are in sedimentary rocks approximately dated to 15 Ma. At this time in the island's vegetational history, individual floras were already quite distinct as macrofossils from different localities suggest various vegetation units. For instance, in Selárdalur (Figures 2 and 4) the most prominent fossil type is *Fagus friedrichii* (Figure 3E). Leaves of this type make up over 90% of the fossils encountered in this outcrop (Grímsson and Denk, 2005; Grímsson and Símonarson, 2006). Other types belong to *Aesculus, Cercidiphyllum, Lonicera, Magnolia, Platanus leucophylla, Rhododendron, Tilia selardalense, Ulmus,* and *Picea* (Áskelsson, 1946a, 1957; Akhmetiev *et al.*, 1978; Grímsson *et al.*, 2007). The Selárdalur flora is thought to represent broadleaved deciduous and partly evergreen beech forests. The sedimentary rocks suggest that this was a highland flora found mainly on well drained slopes. Components of the Selárdalur flora are typical representatives of hardwood forests presently found in a humid warm temperate climate. Interestingly enough, in another outcrop, the Botn locality (Figure 2) of similar age, the strata is composed of fine grained lowland sedimentary rocks, mostly lignite, and the plant fossils found there are mainly conifers. Most prominent taxa encountered are *Sequoia abietina* and *Glyptostrobus europaeus* (Grímsson *et al.*, 2007). It is believed that *Glyptostrobus* was present on floodplains and that *Sequoia* occupied dryer regions (mostly on hummocks). This lowland flora is likely to have merged with a hardwood forest similar to the Selárdalur flora at higher elevation.

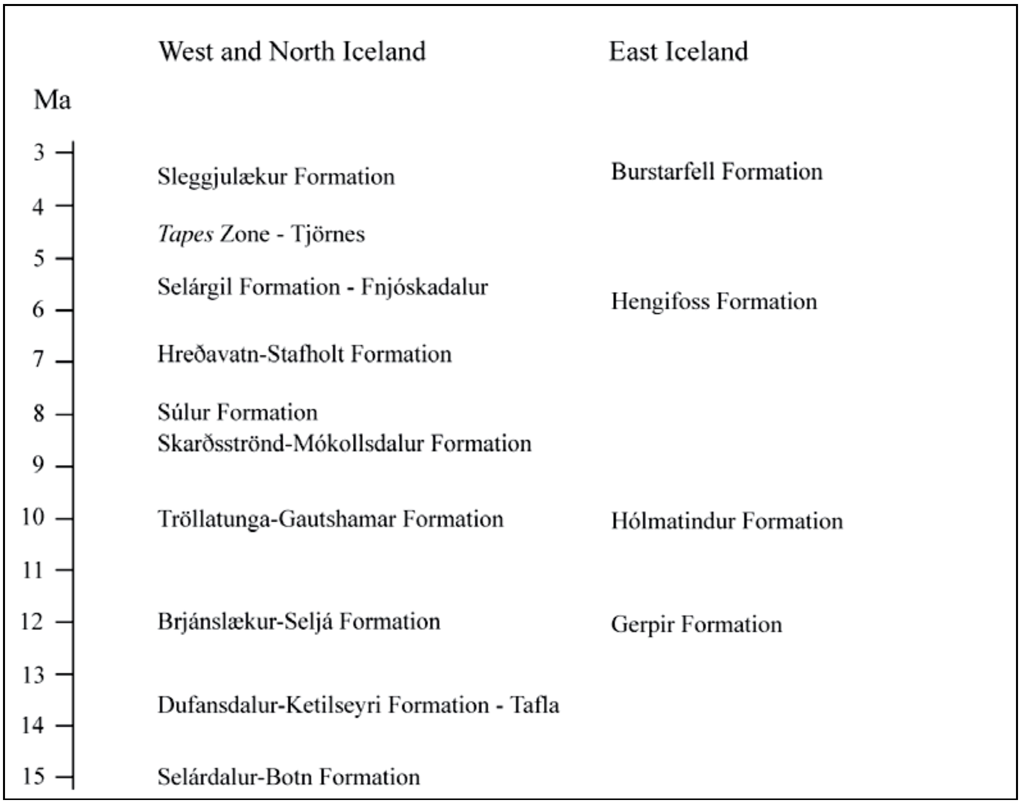

Figure 4. Chronology of the Upper Tertiary sedimentary formations and biozones mentioned in the text. They are both west and east of the volcanic zone. - *Aldursröð jarðmyndana með steingervingum frá efri hluta tertíertímabils sem greint er frá í texta. Þær eru sitt hvoru megin gosbeltisins.*

Only a few floras have been recorded from sedimentary rocks deposited at 13.5 Ma, but they are rather badly preserved. Macrofossils from the Tafla outcrop at Ketilseyri (Figures 2 and 4) are mostly of the same taxon as those found in the older Selárdalur flora (Símonarson *et al.*, 2000, 2002; Grímsson and Símonarson, 2006), with *Fagus friedrichii* being the most prominent. Some of the taxa known from Selárdalur have not been recorded from Tafla, namely *Cercidiphyllum* and *Aesculus*. Judging from the macrofossils and pollen (Akhmetiev *et al.,* 1978) there does not seem to have been any major change in either the vegetation or the climate between 15 and 13.5 Ma (Grímsson *et al.*, 2007).

Plant fossils from Brjánslækur and Seljá, dated to 12 Ma (Figure 4), represent the richest flora known from Iceland (Friedrich, 1966; Denk *et al.,* 2005; Grímsson, 2007b). Modern living analogues of the fossil taxa suggest that the vegetation thrived in a moist, warm-temperate to temperate climate. The woody vegetation at this time was dominated by broadleaved deciduous trees, mixed with conifers and some evergreen taxa. The most common fossils from Brjánslækur (Figure 2) are *Alnus cecropiifolia, Betula islandica,* and *Acer crenatifolium* subsp. *islandicum.* Other macrofossils include *Acer askelssonii, Alnus gaudinii, Carpinus, Comptonia hesperia, Corylus, Fraxinus, Juglans, Laurophyllum, Lonicera, Magno-*

lia, Rosaceae, *Salix gruberi, Sassafras ferrettianum, Smilax, Ulmus* cf. *pyramidalis, Phragmites, Abies steenstrupiana, Cathaya, Cryptomeria anglica, Picea* sect. *Picea, Equisetum, Dryopteris,* and *Osmunda parschlugiana* (Heer, 1868; Áskelsson, 1946b, 1954, 1956; Friedrich, 1966; Akhmetiev *et al.*, 1978; Denk *et al.*, 2005; Grímsson, 2007b).

In the Seljá flora (Figure 2) most abundant fossil types are *Salix gruberi, Alnus cecropiifolia,* and *Populus*. Over 90% of the broadleaved-type fossils collected from Seljá belong to one of these three taxa (Grímsson, 2007b). Other fossils frequently found belong to *Phragmites* and *Equisetum*. Additional fossils have been identified as *Alnus* cf. *kefersteinii, Betula islandica, Carpinus, Pterocarya, Magnolia*, Rosaceae, and *Acer crenatifolium* subsp. *islandicum*.

Sedimentary rocks at Seljá and Brjánslækur suggest that the surrounding region consisted of lowland and highland environment with an extensive river system, floodplains, oxbow lakes, several small lakes and ponds, as well as swamps. The lowlands were surrounded by highland hillsides with valleys and volcanic mountains. At Seljá the macrofossils indicate an azonal riparian flora, with *Alnus, Salix,* and *Populus* growing along rivers and streams (wetland vegetation). In areas with stagnant water *Phragmites* and *Equisetum* became more prominent. Close by on slightly more elevated areas the vegetation included *Acer, Betula, Carpinus, Corylus, Pterocarya, Magnolia*, and Rosaceae (riverbank woodland) (Grímsson, 2007b). At Brjánslækur the macrofossils indicate a shallow lake environment with azonal and zonal vegetation. The shores of the lakes were occupied by herbaceous aquatic and semi-aquatic plants: *Equisetum, Phragmites, Osmunda,* and *Dryopteris* (wetland vegetation). Close to the shoreline, woody plants adapted to wet ground became prominent: *Salix, Alnus, Betula,* and *Acer* (lakeshore woodland). The vegetation cover became denser and additional broadleaved and conifer species became prominent. The zonal forest around the lake was a mixed broadleaved coniferous forest with occasional evergreen trees (Grímsson, 2007b). Additional taxa included *Magnolia, Sassafras, Comptonia, Smilax, Laurophyllum, Liriodendron*, Rosaceae, *Corylus, Fraxinus, Juglans, Lonicera, Carpinus, Ulmus, Abies, Cathaya, Picea*, and *Tsuga* (mixed forests).

The plant bearing formation in Gerpir, East Iceland (Figures 1 and 4), that contains pollen, spores, and rare macrofossils is of similar age as the Brjánslækur-Seljá Formation, which is dated to about 12 Ma (McDougall *et al.*, 1984; Akhmetiev *et al.*, 1978).

The Icelandic vegetation at 10 Ma is represented in many fossil-rich outcrops. In spite of the numerous localities, these floras are much less diverse than the Brjánslækur and Seljá floras (12 Ma). At Tröllatunga (Figures 2 and 4) some of the best-preserved plant fossils in Iceland have been found. The sedimentary rocks at Tröllatunga are rich in warm temperate to temperate taxa; the most common types belong to *Acer crenatifolium* subsp. *islandicum* and *Rhododendron* aff. *ponticum*. For the first time, small leaved *Vaccinium* and *Arctostaphylos* are present and quite common (Denk *et al.,* 2005). Other woody taxa belong to Juglandaceae (Símonarson, 1991), Betulaceae, and Rosaceae. Sedimentary rocks at the nearby Húsavíkurkleif locality (Figure 2), are mostly composed of fossils from ferns and fern allies and the few woody taxa belong to *Salix gruberi, Pterocarya* and *Alnus cecropiifolia* (Grímsson and Denk, 2007). The fossil floras from Tröllatunga and Húsavíkurkleif give information on both zonal and azonal vegetation, indicating mixed coniferous and broadleaved warm temperate to temperate forests. Fossil occurrence and sedimentary rocks suggest that *Salix, Alnus,* and *Pterocarya* grew on banks along rivers. Other hardwood taxa were dominant on drier ground, with other juglandaceous types, *Rhododendron, Acer*, and coniferous taxa (Denk *et al.*, 2005; Grímsson, 2007b; Grímsson and Denk, 2007).

The Hólmatindur Formation in East Iceland (Figures 1 and 4), which contains pollen, spores, and few macro remains, is of the same age, 10 Ma (Meyer and Pirrit, 1957; Akhmetiev *et al.,* 1978).

Hrútagil in Mókollsdalur (Figures 2 and 4) is the best know macrofossil locality from the 9–8 Ma formation. The Hrútagil flora is composed of *Acer crenatifolium* subsp. *islandicum, Acer askelssonii, Alnus cecropiifolia, Alnus* cf. *kefersteinii, Betula cristata,* *Betula subnivalis, Carpinus, Corylus, Fagus gussonii, Juglandaceae, Lonicera, Populus, Pterocarya, Salix gruberi, Ulmus pyramidalis, Phragmites,* Bryophyta, *Picea* sect. *Picea*, and *Pseudotsuga* (Friedrich *et al*., 1972; Akhmetiev *et al*., 1978; Denk *et al*., 2005; Grímsson and Denk, 2007). It is noteworthy that *Fagus gussonii* is recorded for the first time in these 9–8 Ma sediments. This beech species was previously only known from Late Miocene sediments in southern Europe. Its presence in Iceland might suggest migration from continental Europe after accumulation of the 10 Ma sediments (Grímsson and Denk, 2005), but it cannot be excluded that it is a new species that evolved in Iceland parallel to *Fagus gussonii* in Eurasia (Grímsson and Símonarson, 2006). Fossiliferous outcrops from this time reflect different vegetation units of both zonal and azonal origin. Most fossils belong to deciduous broadleaved taxa but some outcrops are richer in conifer remains. The fossil flora from this time suggests mixed conifer and broadleaved deciduous forests of temperate affinity.

Icelandic floras from the Late Miocene (7–6 Ma) are quite different from the 15 and the 12 Ma floras. All the warm-temperate taxa are missing and more cold adapted taxa dominate (Heer, 1868; Akhmetiev *et al*., 1978; Grímsson, 2002). Floras from this time are quite numerous and no other time period in the Miocene of Iceland is represented by so many fossiliferous outcrops. In sedimentary rocks around Lake Hreðavatn (Figures 2 and 4) *Betula cristata* (Lindquist, 1947) is by far the most common fossil found. Other prominent woody plants are *Alnus, Salix, Acer* (Símonarson and Friedrich, 1983), and *Abies*. The flora and sedimentary rocks from this time suggest lacustrine vegetation, and *Betula, Alnus, Salix*, and *Populus* growing close to the shoreline (Grímsson, 2002). The high amount of dispersed coniferous remains of *Abies, Picea, Pinus, Pseudotsuga*, and *Larix* suggests that conifer-dominated woodland forested the highlands surrounding the basins. The vegetation at this time was a temperate to cool-temperate mixed boreal forest.

Fossiliferous localities from the latest Miocene are rather scarce and Selárgil in Fnjóskadalur, North Iceland (Figures 1 and 4) is one of few. The Fnjóskadalur flora (5.5 Ma) is relatively poor in species (Sigurðsson, 1975). The most common fossils are *Salix* leaves and for the first time small-leaved *Salix* are recorded. Other taxa rarely found are *Alnus, Betula* and *Abies*, whereas *Equisetum* and *Phragmites* are common. This flora suggests a cool-temperate, mixed boreal forest.

The Hengifoss Formation in East Iceland (Figures 1 and 4), which contains pollen, spores, and few macro remains, is of similar age or slightly older as it has been dated to 5.7 Ma (McDougall *et al.,* 1976; Akhmetiev *et al*., 1978).

From 6–3 Ma *Betula* and *Salix* shrubs and grasses became more and more common whereas the forest declined, as indicated by the Sleggjulækur flora in West Iceland (Figures 1, 2, and 4) and the Pliocene Tjörnes flora in North Iceland (Akhmetiev *et al*., 1978).

CLIMATIC CHANGES

Fossil plants from the Miocene–Pliocene of Iceland indicate that a humid warm temperate climate with no dry season and warm summers (Cfa climate of Köppen, 1936) prevailed in Iceland between 15 and 10 Ma. The disappearance of important taxa between 12 and 10 Ma, between 10 and 9–8 Ma, and again between 8 and 7–6 Ma, was most likely the result of gradual cooling and indicates the change from a warmer to a cooler summer (change from Cfa to Cfb climate of Köppen, 1936; Denk *et al.,* 2005).

The 15 Ma floras with typical taxa like *Sequoia, Fagus, Cercidiphyllum*, and *Tilia*, grew under a mild and moist climate. The presence of warmth loving taxa such as *Cryptomeria, Sassafras, Liriodendron*, and *Magnolia* in the 12 Ma floras strongly indicates an increase in mean annual temperature as compared to the 15 Ma floras. The climate became considerably warmer at 12 Ma and the mean annual temperature was 12–15°C during this time. In the 10 Ma floras cooler types began to coexist with warm temperate taxa, signaling decreasing temperatures beween 12 and 10 Ma (Denk *et al.,* 2005). The younger, Late Miocene floras at 8–5 Ma that are increasingly dominated by Betulaceae, Salicaceae, and conifers suggest further climate cooling (change towards Cfb and Cfc climates of Köppen, 1936).

Still younger 6–3 Ma floras indicate further cooling that finally resulted in an arctic climate with no true summer (ET climate of Köppen, 1936) and the beginning of perennial ice formation, marking the onset of the last ice age.

SUMMARY

Icelandic non-marine sediments contain both fossilized plants, and remains of invertebrates and vertebrates. The oldest fossils are from the Middle Miocene, approximately 15 million years old, and can be found at outermost parts of the Northwest Peninsula. Younger fossils are known from sedimentary formations between lava flows on either side of the active volcanic zone and decrease in age towards the middle of the island.

The Tertiary sediments are rather rich in plant fossils and a considerable number of floras and vegetation types are known from the Miocene and Pliocene of Iceland. Animal fossil are not as common. Some freshwater animals like sponges, crustaceans, gastropods, and bivalves as well as insects have been collected, but only a few fragmentary bones of terrestrial vertebrates.

Plant fossils reflect part of the vegetation that grew in Iceland millions of years ago, and based on them it was possible to conclude about the palaeo-climate. Furthermore, the composition of woody taxa shows that island was covered with various broadleaved and coniferous forests. Modern living analogous of the fossil taxa presently thrive at southern latitudes in a warm-temperate climate. It has been assumed that when the Iceland climate was at its maximum the mean annual temperature was approximately 10°C higher than it is now. Apparently the precipitation was more or less constant throughout the year.

It is not known exactly when plants colonized Iceland, as the oldest sedimentary rocks are only about 15 million years old, but it is likely that plants lived on proto-Iceland from the beginning, shortly after the opening of the northern North Atlantic. It is assumed that older fossiliferous sediments and fossils can be found below sea level on the Icelandic shelf and further in the west (towards Greenland) and the east (towards the Faeroe Island).

The oldest Icelandic floras are distinguishable from other coeval floras of nearby continents. Here a number of endemic species occur and the composition of the floras changes considerably as they get younger. The change in species composition seems in direct correlation with gradual cooling of climate in the late Cainozoic. The number of thermophilous species decreased when the Miocene came to an end. The cooling climate as well as continuous isolation of Iceland in the North Atlantic is believed to have had strong affects on the evolution of the islands palaeobiota.

Acknowledgements

We would like to thank Dr. Margrét Hallsdóttir, Icelandic Institute of Natural History, Dr. Ole Bennike, GEUS, and Dr. Leó Kristjánsson, Institute of Earth Sciences, University of Iceland, for valuable comments on the manuscript. The University of Iceland Research Fund and Rannís are thanked for financial support.

ÁGRIP

Í íslenskum setlögum hafa fundist plöntuleifar ásamt leifum hryggleysingja og hryggdýra. Elstu steingervingar landsins eru um 15 milljón ára (frá því um miðbik míósentíma) og hafa fundist á ystu nesjum Vestfjarða. Yngri lífveruleifar hafa síðan fundist í setlagasyrpum milli hraunlaga sitt hvoru megin gosbeltisins og yngjast er nær dregur miðju landsins.

Íslensk tertíerlög eru frekar auðug af plöntusteingervingum og töluverðum fjölda gróðurfélaga hefur nú þegar verið lýst úr íslenskum setlögum. Töluvert minna hefur fundist af dýraleifum. Einkum hafa fundist leifar ferskvatnsdýra eins og svampa, krabbadýra, snigla og samlokna svo og skordýra, en einungis örfá brot úr beinum landhryggdýra.

Plöntuleifarnar endurspegla hluta af þeim gróðri sem óx hér fyrir milljónum ára og af þeim má sjá hvers konar loftslag ríkti hér á landi á míósen- og plíósentíma. Tegundafjöldi viðarplantna, sem fundist hafa, sýna að hér uxu bæði laufskógar og barrskógar. Núlifandi tegundir, sem eru skyldastar íslensku

tertíerplöntunum, þrífast nú mun sunnar og vaxa þar og dafna í heittempruðu loftslagi. Gera má ráð fyrir að ársmeðalhiti hafi verið um 10°C hærri en nú þegar loftslag var hlýjast á míósentíma fyrir um 12 milljónum ára og úrkoma verið jafndreifð á árið.

Ekki er nákvæmlega ljóst hvenær plöntur námu land á Íslandi þar sem elstu setlög landsins eru vart eldri en 15 milljóna ára. Hins vegar verður að telja líklegt að plöntur hafi þrifist á frum-Íslandi alveg frá upphafi, stuttu eftir að norðurhluti Norður-Atlantshafs tók að myndast. Ætla má að eldri setlög með steingervingum finnist neðansjávar í setlögum á landgrunni Íslands og áfram til vesturs (til Grænlands) og austurs (til Færeyja).

Elstu gróðurfélög landsins sýna ákveðin sérkenni ef þau eru borin saman við gróðurfélög úr jafngömlum setlögum á meginlöndunum. Hér hafa myndast nokkrar einlendar (séríslenskar) tegundir og töluverður munur er á misgömlum félögum plantna. Breytingar á þeim virðast vera í nánu sambandi við hægfara kólnun loftslags á síðari hluta nýlífsaldar. Kulvísum tegundum fór fækkandi þegar líða tók á jarðsöguna og breytingar á loftslagi og síaukin einangrun Íslands í Norður-Atlantshaf setja sterkan svip á þróun gróðurs og dýralífs.

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