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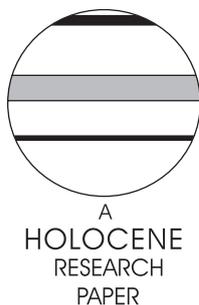
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# The late-Holocene vegetation history of the Central Caspian (Hyrceanian) forests of northern Iran

Elias Ramezani,<sup>1, 2\*</sup> Mohammad R. Marvie Mohadjer,<sup>2</sup> Hans-Dieter Knapp,<sup>3</sup> Hassan Ahmadi<sup>2</sup> and Hans Joosten<sup>1</sup>

(<sup>1</sup>Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt-University, Grimmer Straße 88, D-17487 Greifswald, Germany; <sup>2</sup>Faculty of Natural Resources, University of Tehran, Karaj, Iran; <sup>3</sup>International Nature Conservation Academy, (Isle of) Vilm, D-18581 Putbus, Germany)

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**Abstract:** Pollen analysis of the peat in a small mire on the northern slope of the Alborz Mountains (550 m a.s.l.) in the Central Caspian forests of Iran reveals changes in forest and wetland vegetation during the last millennium. A forest, principally of *Alnus* and *Carpinus* occurred over almost the whole period. *Quercus*, *Ulmus* and *Parrotia* were less common, while *Fagus*, *Pterocarya*, *Acer* and *Diospyros* fluctuated as a probable result of human interference and/or climatic change. Two phases of clay deposition in the mire can be dated to the 'Mediaeval Climatic Anomaly' (AD 1100) and the beginning of the 'Little Ice Age' (AD 1560–1600). Although human activity seems to have persisted in the region during the whole of the past millennium, increased NAP values point to intensified human interference since the beginning of the nineteenth century.

**Key words:** Vegetation history, pollen analysis, Caspian (Hyrceanian) forests, late Holocene, human impact, Alborz Mountains, Iran.

## Introduction

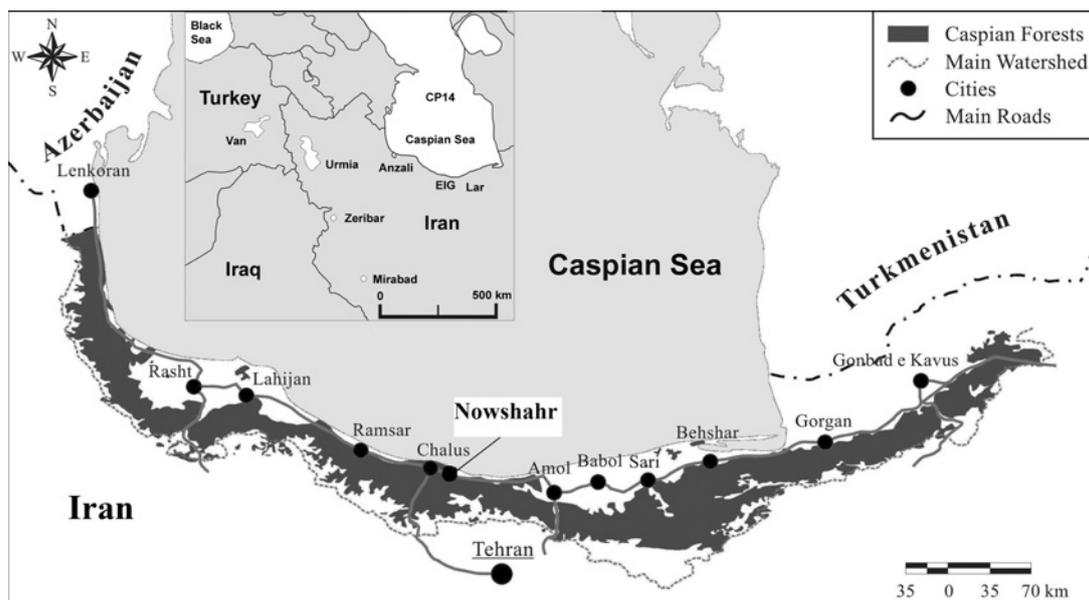
Deciduous broadleaved forests are the natural vegetation of the temperate regions of eastern North America, western Eurasia and eastern Asia. Human activities have severely reduced their areas, and the remaining forests are largely plantations and secondary woodlands. Relics of primary temperate broadleaf forests are rare all over the world (Peterken, 1996; Knapp, 2005).

Many elements of the Arcto-Tertiary flora, such as *Parrotia persica* (the last representative of a widespread and species-rich genus in the Tertiary), *Pterocarya fraxinifolia* and *Zelkova carpinifolia*, which were widespread over the entire temperate zone of the Northern Hemisphere during the Pliocene, became extinct in Europe and northern Asia during the Pleistocene (Zohary, 1963, 1973; Ehlers, 1996–2007b). The Caspian (Hyrceanian) forests on the southern Caspian coastal plain and the northern slopes of the Alborz and Talysh Mountains (Iran, Azerbaijan, Figure 1) constitute – together with the Colchic forests in Georgia – the most important refugia and the last relics of primary temperate deciduous broadleaved forests worldwide

(Bobek, 1951; Walter, 1985; Röhrig, 1991; Walter and Breckle, 1991; Schroeder, 2002; Knapp, 2005) and constitute a model for the Pliocene vegetation of Europe (cf. Leroy and Roiron, 1996).

Despite the outstanding palaeoecological significance of the Caspian forests, the Pleistocene and Holocene vegetation history of this region is hardly known. In fact, almost all conclusions regarding the Tertiary relict flora and the climatic history of this region are extrapolated from fossil finds outside the region and/or from biogeographical and floristic analyses of recent plant species (Ehlers, 1996–2007b). On that basis, Bobek (1955) concluded that the mountains and highlands of northern Iran experienced a temperature drop of 4–5°C at most during the last glacial period, and he assumed a markedly dry period from c. 9000 to 4000 BC for the South Caspian area, parallel to the climatic optimum in Europe. This desiccation would have led to a 200 m upward displacement of the Caspian lowland forest, but it would have left unaffected the forest higher in the mountains. Similar cold dry climatic conditions have been inferred from Lateglacial isotope and early-Holocene pollen records from western Iran (Lakes Zeribar, Mirabad, Urmia), Turkey, the Near East, Georgia, and southwestern Siberia and are consistent with palaeoclimate models that indicate dry early-Holocene conditions in continental interiors

\*Author for correspondence (e-mail: elias.r@uni-greifswald.de)



**Figure 1** The distribution of the Caspian forests in Iran (modified after Nosrati *et al.*, 2005), showing the location of the EIG mire and other sites mentioned in text

(Wright *et al.*, 2003). Kazancı *et al.* (2004) concluded from a study on the sedimentary and environmental characteristics of Lake Anzali in northern Iran (Figure 1) that a dry, wind-dominated climate prevailed in that region at 10 000–8000 BP.

In contrast to the nearby Caucasus region, where palynological studies have elucidated the general vegetation history (see, among others: Yazvenko, 1991, 1994; Kvavadze, 1993; Stuchlik and Kvavadze, 1993, 1995; Kvavadze and Efremov, 1995; Connor *et al.*, 2004, 2007), Quaternary palaeoecological studies in Iran have mainly concentrated on the dry parts of (western and north-western) Iran, including Lake Zeribar (see, among others: van Zeist and Wright, 1963; Megard, 1967; van Zeist, 1967; Wasylkova, 1967, 2005; Wright *et al.*, 1967; Freitag, 1977; van Zeist and Bottema, 1977, 1991; El-Moslimany, 1986, 1987; Stevens *et al.*, 2001, 2006), Lake Urmia (Bottema, 1986) and Lake Mirabad (Griffiths *et al.*, 2001; Stevens *et al.*, 2006). These studies indicate that during the late Pleistocene the Zagros Mountains in western Iran were dominated by *Artemisia* and *Chenopodiaceae*, which represent the semi-desert vegetation of a cold, dry climate. At the beginning of the Holocene, a more temperate and more humid climate prevailed, grasses replaced the *Chenopodiaceae-Artemisia* assemblage, and pistachio and oak gradually migrated into the region. In this period the seasonal distribution of precipitation was not the same as today, ie, spring rains were rare, if any, and hence summer drought was more prolonged. The modern climatic regime prevailed by the mid Holocene (6000–5500 BP) and the present-day Zagros forest has been established since then (El-Moslimany, 1986; Stevens *et al.*, 2001; Wright *et al.*, 2003). The long history of felling, grazing and clearing led to severe vegetation degradation (Wright *et al.*, 1967; Frey and Probst, 1986; Sagheb-Talebi *et al.*, 2004).

In northern Iran some palynological studies have been made on marine sediments to reconstruct Caspian Sea-level fluctuations (Leroy *et al.*, 2000). A pollen diagram from a 140 cm pilot core (ie, CP 14 in Figure 1) from the southern Caspian basin in 330 m water depth shows for the Holocene a relatively stable open steppe to semi-desert landscape dominated by *Chenopodiaceae* and *Artemisia*. The few arboreal pollen grains in the core were interpreted to have come from the Caucasus and Alborz Mountains. Kazancı *et al.* (2004), studying sediment cores and surface samples

from Lake Anzali (Figure 1) reconstructed the sea-level fluctuations and long-term transgressions of the Caspian Sea over the last millennia. From the non-marine sediments, especially a loess-soil complex, they suggested that a dry and windy climate prevailed in the area at 10 000–8000 BP. From early-Pleistocene sediments of Lake Lar (2600 m a.s.l.) on the climatically dry south slope of the Damavand volcano (Figure 1) von der Brelie (1961) concluded that the vegetation around the lake had been steppe-like and the climate slightly warmer than today. Because of the scarcity of pollen in his core, however, no pollen diagram was constructed. The only attempt to elucidate the Holocene vegetation history of the Caspian forests is Djamali's study (in progress) on the sediments of two lakes in the easternmost and central parts of the Caspian region (Morteza Djamali, personal communication, 2006).

This paper presents the first pollen diagram from the central Caspian region covering the last millennium of the Holocene, interprets the diagram in terms of forest composition, structure and dynamics, and discusses the possible roles of humans and climate in these changes.

## The Caspian forest

Within the Euro-Siberian phytogeographical region, the Hyrcanian province covers the southern Caspian coastal plain and the northern slopes of the Alborz (also called 'Elburz' or 'Alburz') Mountains in northern Iran and southeastern Azerbaijan (Zohary, 1963, 1973; Browicz, 1989). The province is characterized by the predominantly summer-green broadleaved Hyrcanian (Caspian) forest, which extends from the Caspian lowlands up to 2500 m (in some places up to 2800 m) elevation and from east to west over an area of 1 900 000 ha (Figure 1) (Sabeti, 1994; Sagheb-Talebi *et al.*, 2004). On the northern slope of the Alborz Mountains it shows a conspicuous altitudinal zonation (cf. Sabeti, 1994; Knapp, 2005):

### Hyrcanian low- and mid-altitude forests (up to c. 1000 m a.s.l.)

These forests consist mainly of alder and oak. On moist soils *Alnetum*, *Alneto-Pterocaryetum*, *Populetum* and *Populeto-Alnetum* communities with *Alnus glutinosa*, *Pterocarya fraxinifolia* and

*Populus caspica* dominate. Common tree species include *Zelkova carpinifolia*, *Acer velutinum*, *A. cappadocicum*, *Fraxinus excelsior* subsp. *coriariifolia*, *Tilia platyphyllos*, *Ulmus minor* (= *U. carpinifolia*), *U. glabra*, *Diospyros lotus*, *Gleditschia caspica*, *Ficus carica*, *Salix* spp., *Fagus orientalis* and *Juglans regia*. Important shrubs are *Mespilus germanica*, *Punica granatum* and *Prunus divaricata*, lianas include *Vitis sylvestris*, *Smilax excelsa*, *Hedera pastuchowii*, *Humulus lupulus* and *Jasminum officinale*. All valleys and riversides, from the plains up to 1000 m, are covered by Alnetum with a dominance of *Alnus subcordata*. On well-drained soils of the plain are Quercetum, Querceto-Carpinetum and Buxetum communities with *Quercus castaneifolia*, *Carpinus betulus* and *Buxus hyrcana*. The tree, shrub and liana species mentioned above occur here as well and are complemented by the evergreen *Laurocerasus officinalis*, *Ilex spinigera* (= *I. aquifolium*) and *Ruscus hyrcanus*. The oak forests extend up to 1000 m a.s.l., whereas Parrotietum and Parrotio-Carpinetum communities (with *Parrotia persica*) encompass a belt below 500 m elevation.

### The beech forests

At altitudes between (700) 1000 and 2000 m, beech forests (Fagetum, Fageto-Carpinetum or Carpineto-Fagetum) prevail. Here *Fagus orientalis* and *Carpinus betulus* are the dominant species, while *Acer velutinum*, *A. cappadocicum*, *Tilia platyphyllos*, *Ulmus minor*, *U. glabra*, *Cerasus avium*, *Taxus baccata*, *Fraxinus excelsior* subsp. *coriariifolia* and *Sorbus torminalis* are less common.

### High mountains oak forests

The high Alborz Mountains, 2000–2500 (2800) m a.s.l., are covered by subhumid high mountains oak forests (Quercetum, Querceto-Carpinetum and Carpineto-Quercetum) with dominant *Quercus macranthera*, *Carpinus orientalis*, and *C. schuschaensis* accompanied by *Acer campestre*, *A. hyrcanum*, *Viburnum lantana* and *Lonicera* spp.

Some relict vegetation is not included in this classification. *Cupressus sempervirens* var. *horizontalis*, for instance, is found in a few localities associated with *Acer monspessulanum*, *Celtis australis*, *Paliurus spina-christi* and *Crataegus microphylla* (= *C. monogyna*). Their sporadic and isolated occurrence suggests that these Cypress forests are remnants of an Old-Mediterranean vegetation type, perhaps much older than the true Hyrcanian one (Zohary, 1963, 1973; Sabeti, 1994).

Because of its remoteness, inaccessibility and unhealthy climate (malaria!), the Caspian forest remained largely unexploited until the mid-nineteenth century, when charcoal was shipped in large quantities across the Caspian Sea to Baku and other Russian ports. The most decisive impacts on the Caspian forests came with the construction of all-weather roads across the Alborz Mountains in AD 1920. The rapid expansion of Tehran created huge demands for charcoal and timber for construction, leading to a rapid depletion of the easily accessible tracts of the Caspian forest belt. Only in 1958 was the production of charcoal officially forbidden. The nationalization of all forests after 1963 was a major step in the preservation of the remaining forests (Ehlers, 1996–2007a; Abdollahpour and Assadi Atui, 2005). Today the Caspian lowlands, with the exception of a few patches of preserved natural habitats, have been turned almost completely into agricultural lands (especially rice paddies and tea plantations) and citrus and, more recently, kiwi fruit orchards. The foothills of the Alborz and its slopes, in contrast, still have considerable forest cover. These sections have also experienced selective exploitation through forestry, forest pasture and various forms of individual tree cutting (de Planhol, 1969; Frey and Probst, 1986; Sabeti, 1994; Knapp, 2005; Seifollahian *et al.*, 2005). However, it should be emphasized that vegetation destruction in Iran has been much less than

in other countries of southwest Asia (Frey and Probst, 1986). In northern Iran at least 100 000 ha of the Caspian forests have remained untouched and are considered to be pristine forest (Knapp, 2005; Sperber, 2005).

### The site

The investigated site, EIG mire (called Muzidarbon by local people) (36°33'N, 51°29'E), is 3000 m<sup>2</sup> in area and lies in the Mashalak Forest on the northern slope of the Central Alborz Mountains, 15 km south of Nowshahr (=Noshahr) at an elevation of 550 m a.s.l. (Figure 1). The bedrock is predominantly limestone (Forest, Range and Watershed Organization of Iran (FRWO), 1997), so the mire may have been formed as a karst sinkhole. A small stream flows through the mire. The mire is situated on a local plain and surrounded by a mosaic of the communities *Carpinus betulus*-*Acer velutinum*-*Alnus subcordata*, *C. betulus*-*Parrotia persica* and *Pterocarya fraxinifolia*-*A. subcordata* (FRWO, 1997). Locally dense *Diospyros lotus* occurs where the tree canopy is relatively open. Other common trees include *Quercus castaneifolia*, *Tilia platyphyllos*, *Acer cappadocicum*, *Ulmus glabra* and, especially in higher elevations, *Fagus orientalis*.

Organized forestry has been working in the area in the last 45 years. Scattered recently felled tree stumps were observed in the vicinity of the mire. A few clearings (1000–1500 m<sup>2</sup> in area) were seen during field work in May 2005. Grazing by cattle and sheep/goats is substantial in the area.

The current vegetation of the mire consists of *Sparganium erectum* (the most frequent species), *Equisetum* sp., several Poaceae (eg, *Microstegium vimineum*, *Oplismenus* cf. *undulatifolius*), *Carex* spp. (including *C. pendula*), *Mentha aquatica*, *Thelypteris palustris*, *Rumex* spp., *Urtica dioica*, *Ranunculus* sp., *Lythrum salicaria*, *Juncus* sp., *Nasturtium officinale* and *Polygonum* sp. In the wetter central part of the mire, *Lemna* (cf. *minor*) covers the surface. *Carpinus betulus*, *Alnus subcordata*, *Tilia platyphyllos*, *Acer velutinum*, *A. cappadocicum*, *Diospyros lotus* and *Ficus carica* grow near the mire.

There are no climatic records available for the site directly. The nearest location of a weather station (Nowshahr, –20 m a.s.l.) shows a mean annual temperature of 16.1°C, a mean temperature of the coldest month (February) of 2.3°C, and a mean of the warmest month (August) of 29.2°C. Mean annual precipitation is 1310 mm, and mean annual minimum and maximum relative humidity is 75 and 95%, respectively (data provided by the meteorological station of Nowshahr).

### Materials and methods

A 4.5 m sediment core of peat over clay and gyttja was collected with a chamber corer (50 cm length, 5 cm diameter) from the centre of the EIG mire in May 2005. The cores were wrapped in plastic film, placed in half PVC tubes, and stored at 4°C.

Pollen samples of 0.5 (–1.5) cm<sup>3</sup> were taken at (5–) 10 cm intervals and are referred to by their actual depth below surface (cm). *Lycopodium* tablets were added to the samples in order to calculate pollen concentrations (grains/cm<sup>3</sup>) (Stockmarr, 1971). Sample preparation followed standard techniques (cf. Fægri and Iversen, 1989) and included treatment with HCl and KOH, sieving (120 µm), treatment with HF, acetolysis (7 min) and mounting in silicon oil (2000 centistokes).

Counting was carried out with a Zeiss Axiolab microscope with 400 × magnification. Pollen-morphological types are displayed in the text by SMALL CAPITALS in order to clearly distinguish them from plant taxa (Joosten and de Klerk, 2002). Common pollen and

spores (Appendix 1) were identified with and named after Moore *et al.* (1991), Beug (2004), and the Northwest European Pollen Flora (Punt, 1976; Punt and Clarke, 1980, 1981, 1984; Punt *et al.*, 1988, 1995, 2003; Punt and Blackmore, 1991) with aid of the reference collection of the Institute of Botany and Landscape Ecology of Greifswald University and that of the first author. *PTERIS CRETICA* was identified with help of figures of Reille (1992) and the reference collection. Other palynomorphs were identified with van Geel (1978, 1986), van Geel *et al.* (1980/81, 1982/83, 1989), van der Wiel (1982), Ellis and Ellis (1997) and Charman *et al.* (2000). Types not described in these studies are defined in Appendices 2 and 3.

For calculation and presentation of the palynological data we used the computer programs TILIA 1.12, TILIA GRAPH 1.18 and TGView 1.5.1/2.0.2 (Grimm, 1992, 2004). Microfossil frequencies were calculated relative to a pollen sum including pollen types that are assumed to originate from trees, shrubs, lianas (AP) and upland herbs (NAP). Pollen types that might be produced by wetland herbs (eg, WILD GRASS GROUP and CYPERACEAE) were excluded from the sum to rule out (extra)local effects that may obscure regional vegetation developments (cf. Janssen and IJzermans-Lutgerhorst, 1973). An attempt was made to reach a pollen sum of at least 400 grains. In a few cases, low concentrations, eg, in samples with a high clastic component, prevented reaching this number.

In the diagrams, pollen types were ordered stratigraphically, and homogeneous zones were distinguished by eye in order to facilitate successional description and interpretation.

For <sup>14</sup>C-AMS dating, three samples of emergent plant macrofossils (Table 1) were treated with 5% KOH (5 min below boiling point, cf. Grosse-Brauckmann, 1986), dried overnight at 40°C and sent to Poznań Radiocarbon Laboratory in Poland. Radiocarbon ages were calibrated with CALIB (Stuiver and Reimer, 1993).

Nomenclature of vascular plants follows Mozaffarian (1998).

## Results and interpretation

### Age determination

For the age–depth model (Figure 2) we have assumed constant accumulation rates between the calibrated dates listed in Table 1. Although it is improbable that sedimentation was really constant, as evidenced by the inwashed clastic material (Table 2 and see Figure 4), without additional dates a linear age–depth model seems to be the most suitable one.

### Forest compositional changes

The upland diagram (Figure 3) is characterized by the dominance of *ALNUS* and *CARPINUS* pollen and other pollen types of mesic forest trees, such as *FAGUS*, *PTEROCARYA FRAXINIFOLIA*, *ULMUS GLABRA*, *PARROTIA PERSICA* and *QUERCUS*. Seven pollen assemblage zones are distinguished.

#### *Zone EIG-A (FAGUS-PTEROCARYA FRAXINIFOLIA-zone, 450–405 cm; before c. AD 1100)*

This zone is characterized by high values of *FAGUS* and *PTEROCARYA FRAXINIFOLIA* TYPE and rather low values of *ALNUS* and *CARPINUS*. Present with relatively low values (ie, 2–4%) are *QUERCUS*, *ACER CAMPESTRE*, *ULMUS GLABRA* and *PARROTIA PERSICA* TYPE. Fern spores, including *DRYOPTERIS FILIX-MAS*, *PTERIS CRETICA* and *POLYPODIUM VULGARE*, show high values.

The very high values (up to 52%) of *FAGUS* pollen could reflect an extralocal (cf. Janssen, 1973) occurrence of *Fagus* near the coring site. Currently, small *Fagus* populations occur under special microclimatic conditions also near the mire's elevation, ie, 500–600 m a.s.l., and individual specimens occur even as low as

80 m (Zohary, 1963, 1973; Sabeti, 1994; Sagheb-Talebi *et al.*, 2004). More probably, however, the *FAGUS* values indicate pollen transport from higher elevations. *Fagus*-dominated communities presently prevail in the Central Caspian forests at (900)1000–2000 m a.s.l. The alternative hypothesis of input via water or soil erosion is supported by the silty clay sediment (Table 2), the large proportion of indeterminable grains (Figure 4) and corroded *FAGUS* pollen, the abundance of fern spores with their corrosion-resistant wall structure (cf. Wilmshurst and McGlone, 2005), and the low pollen concentrations in this zone. These features may be attributed to forest soil (indicated by *FAGUS* clumps) and to clastic material washed-in via a mountain stream such as the one that at present feeds the mire basin.

With respect to *PTEROCARYA FRAXINIFOLIA* TYPE, a local or extralocal occurrence of *Pterocarya fraxinifolia* trees seems feasible. Today, pure and mixed stands of this species are quite common in the lower zone of the Alborz Mountains (Zohary, 1973).

#### *Zone EIG-B (ALNUS-CARPINUS-PTEROCARYA FRAXINIFOLIA-zone, 405–275 cm; c. AD 1100–1350)*

*FAGUS* and the fern spore types have abruptly declined, and *ALNUS* reaches the highest value throughout the record (80%). *CARPINUS* also shows high (26–44%) and fairly constant values, except at 370 cm depth, where *ALNUS* peaks (also visible in the pollen-concentration diagram (Figure 5)). *ULMUS GLABRA* TYPE is a minor component among the arboreal pollen types, with the exception of a peak (4.5%) in the middle of the zone. *DIOSPYROS* TYPE is continuously present with low values (maximum 1.4%). *ACER CAMPESTRE* pollen shows a small peak (4.1%) in the mid-part of the zone. Single *JUGLANS REGIA*, *VITIS VINIFERA*, *SALIX*, *HUMULUS LUPULUS* and *FRAXINUS* grains appear in this section.

Over the lower zone boundary, *PTEROCARYA* percentages decrease abruptly, but the type retains rather high values (3–12%) in zone EIG-B. The increased values in the pollen-concentration diagram indicate that *Pterocarya fraxinifolia* still was a prominent element in the local or extralocal forest composition, but that the percentage values of its pollen are suppressed by high values of *ALNUS* and *CARPINUS* TYPE pollen. *Carpinus betulus* and *Alnus subcordata* are among the most frequent trees in the present-day forest communities in the study area (FRWO, 1997, and personal observations).

Insect-pollinated *Diospyros lotus* has low pollen productivity, so its low pollen values may still indicate its abundance in the immediate vicinity of the mire in this period. As this species is favoured by light (personal observations), the relatively high values of this pollen type may reflect human impact. The fruits of *Diospyros* (the date-plum) were used as a sweet and energy-rich food source in the Caspian region (Sabeti, 1994; personal communications with local inhabitants, 2006). The regular occurrence of individual *JUGLANS REGIA* TYPE pollen in this and the next zones may point to human activity in this part of the Caspian forest, particularly because the natural occurrence of *Juglans regia* in this area is questionable (Sabeti, 1994). Human impact is also indicated by *CHENOPODIACEAE* and *ARTEMISIA*, which are continuously present with low values, and by the single occurrences of *AMBROSIA*, *PTERIDIUM AQUILINUM*, *SECALE CEREALE*, *AVENA-TRITICUM* GROUP and *PLANTAGO LANCEOLATA* pollen.

#### *Zone EIG-C (CARPINUS-ALNUS-DIOSPYROS-zone, 275–195 cm; c. AD 1350–1560)*

*CARPINUS* dominates the assemblage, with average values of c. 45%, whereas *ALNUS* with lower values than before is still the second most abundant AP type. The concentration diagram (Figure 5) reveals that the higher values of *FAGUS* are a relative effect of the decrease of *Alnus* and do not reflect an increase of *Fagus* in the forest composition in that period. Low values of *PTEROCARYA FRAXINIFOLIA* are characteristic for this zone. The increased values

of *CARPINUS* and *PARROTIA PERSICA* and the decreased amounts of *ALNUS* and *PTEROCARYA FRAXINIFOLIA* suggest drier conditions compared to the zone before (Zohary, 1973), possibly as a result of climatic change.

Increased values of *DIOSPYROS* and slightly higher values of *PARROTIA PERSICA* (up to 3.2%) may indicate increased human interference with the forest composition. Increased human impact is also suggested by higher values of *ARTEMISIA*, *CHENOPODIACEAE*, *PLANTAGO LANCEOLATA*, *AMBROSIA* and *RUMEX ACETOSELLA* TYPE.

#### Zone EIG-D (deposition of clastic material, 195–175 cm; c. AD 1560–1600)

The zone consists of a clay layer characterized by very poor pollen preservation (cf. the large amount of indeterminable grains, Figure 4) and consequently low pollen sums. *TILIA* and *PTEROCARYA FRAXINIFOLIA* suddenly occur with high values (11% and 7%, respectively). The 'peaks' of *BUXUS* and *VISCUM* and the fluctuating values of *ALNUS* and *CARPINUS* are probably attributable to the low pollen sum. As in zone EIG-A, fern spores (*DRYOPTERIS FILIX-MAS*, *PTERIS CRETICA*, *POLYSTICHUM*, *POLYPODIUM VULGARE*, *MONOLETE SPORES*), *USTULINA DEUSTA* and *MONODICTYS* (Figure 4) are frequent, indicating the in-wash of forest soil (cf. Wilmshurst and McGlone, 2005).

The higher content of clastic material (cf. Figure 4) in this zone compared with the previous one indicates that the clay deposition was due to a single short-term erosional event. Heavy rainfall is at present not extraordinary in this mountainous environment, and both small and large mountain streams run in the surroundings of the mire. The coincidence of the clay deposition (around AD 1560–1600) with the first part of the 'Little Ice Age' (cf. Bradley *et al.*, 2003a) may point to increased precipitation at that time. An (additional?) anthropogenic cause of increased erosion is made plausible by the higher values of anthropogenic indicators in the second part of the previous pollen zone EIG-C. The rather high values of *ARTEMISIA* and *ANTHEMIS* (both 3.6%) in zone EIG-D may support this hypothesis, but they could equally be ascribed to the extremely low pollen sum in the sample concerned and to the corrosion resistance of their pollen wall.

#### Zone EIG-E (*ACER CAMPESTRE-CARPINUS-ALNUS* – zone, 175–85 cm; c. AD 1600–1800)

*ACER CAMPESTRE* suddenly reaches high values of up to 39% and *CARPINUS* and *ALNUS* regain their high, fluctuating values. The low pollen productivity and poor pollen dispersal of *Acer* (Punt and Clarke, 1980; Yazvenko, 1994; Mitchell and Cole, 1998) imply that these pollen percentages indicate the prominent occurrence of *Acer* (cf. *velutinum*) in the immediate surroundings of the mire. *Acer velutinum* and *Alnus* spp. are pioneer species in clearings of the Caspian forests. Currently *Acer velutinum* creates monodominant stands (Sabeti, 1994) when sufficient light reaches the forest floor and the soil is disturbed (personal observation), for example after forest road construction or landslides. The nearest place where a landslide could have happened is located 50–60 m south of the mire on a steep slope. Today, *Acer velutinum* constitutes 13% of the trees of the compartment in which the mire is situated (FRWO, 1997).

#### Zone EIG-F (*ALNUS-ARTEMISIA-CHENOPODIACEAE*–zone, 85–35 cm; c. AD 1800–1940)

Pollen of *ACER CAMPESTRE* TYPE has largely disappeared and the pollen assemblage is dominated by *ALNUS*, *CARPINUS*, *PTEROCARYA*, *FAGUS*, *ULMUS GLABRA* and, to a lesser degree, *QUERCUS* and *PARROTIA PERSICA*. Comparison of the percentage and concentration diagrams shows that the influx of *CARPINUS* and *PARROTIA PERSICA* both increased after the dramatic decline of *ACER CAMPESTRE* (Figures 3 and 5). *Carpinus betulus* and *Parrotia persica* are two opportunistic species that, after felling, vigorously replace *Fagus*,

*Quercus* and other hardwoods in the low and mid elevations of the Caspian forests (Zohary, 1963; personal observation). A possible explanation for the subsequent sharp decline of *CARPINUS* and *PARROTIA PERSICA* in this zone could be the felling of the associated species that produce a good-quality charcoal. Charcoal production was very common practice in several parts of the forests until around 1960. The subsequent expansion of *Alnus*, as a pioneer species, followed by *Fagus*, *Ulmus* and other mesic taxa, seems to reflect natural succession. With a small peak (1.1%) at the beginning, *HUMULUS LUPULUS* shows a regular occurrence in the zone. *Humulus lupulus* is a light-demanding (shade-intolerant) liana that grows naturally in the Caspian region (Sabeti, 1994).

Characteristic are the high values of *CHENOPODIACEAE* and *ARTEMISIA*, which attain their highest values of the entire record (9.6 and 8.4%, respectively) and the consequently low values of AP (76%), particularly close to the upper boundary of the zone. This may either reflect increased regional signals of *Artemisia* spp. and *Chenopodiaceae* expanding in the Caspian lowlands following forest clearance, or the opening of the canopy of the adjacent mountain forest described above. The latter suggestion is supported by increasing values of *ATHYRIUM FILIX-FEMINA* and *MONOLETE SPORES* (Figure 4, zone EIG-6b).

#### Zone EIG-G (*CARPINUS*–zone, 35–0 cm; since c. AD 1940)

A sharp increase of *CARPINUS* TYPE pollen may reflect a successional stage in which the shade-intolerant *Alnus* is replaced by the intermediate shade-tolerant *Carpinus betulus*. *ALNUS* attains values up to 37%, whereas values of *FAGUS*, *ACER CAMPESTRE*, *QUERCUS*, *ULMUS GLABRA* and *PARROTIA PERSICA* remain low. AP first rises to nearly 98% but in the uppermost part, ie, close to the mire surface, drops down to c. 90%. Among the NAP types, *ARTEMISIA* and *CHENOPODIACEAE* are still conspicuous whereas upland fern spores are largely absent.

### Wetland development

Seven pollen/spore assemblage zones and two subzones have been distinguished for the 'wetland' diagram (Figure 4; Appendix 1 provides the types not included in the diagrams).

In EIG-1 (before AD 1100), *MONODICTYS* (TYPE EMA-102, figure 6a–c; see also Appendix 3) has a very prominent peak near the upper boundary of the zone. *Monodictys castanea*, the only *Monodictys* species recorded from Iran (Dr Mehrdad Abbasi, Plant Pests and Diseases Research Institute, Iran; personal communication, 2007), is a Hyphomycete that grows on rotten wood of eg, *Quercus* (Ellis and Ellis, 1997). *MONODICTYS* shows throughout the record a very clear positive correlation with the curve of *PTEROCARYA FRAXINIFOLIA* that may reveal a host–parasite relationship (cf. Figures 3 and 4). *MONOLETE FERN SPORES WITHOUT PERINE* and indicators of eutrophic to mesotrophic conditions (TYPE 143: *DIPOROTHECA*, cf. van Geel and Aptroot, 2006) and shallow, stagnant, oxygen-rich water (TYPE 315: *SPIROGYRA*, cf. van Geel, 2001) are abundant. *USTULINA DEUSTA* (TYPE 44), which peaks in the upper part of the zone, is a parasite causing soft-rot of wood on a variety of host trees; an influence of the fungus on forest succession, however, is unlikely (van Geel and Aptroot, 2006).

*ARCELLA*, *MENTHA*, *CYPERACEAE* and TYPE 201 occur less frequently. The upper boundary of the zone is marked by high values of TYPE EMA-104 (Figure 6d–f; Appendix 3), a fungal spore that according to André Aptroot (personal communication, 2007) can be ascribed to a *Neurospora* (*GELASINOSPORA*-TYPE). In the upper part of this zone the silty clay gradually changes to a highly organic gyttja.

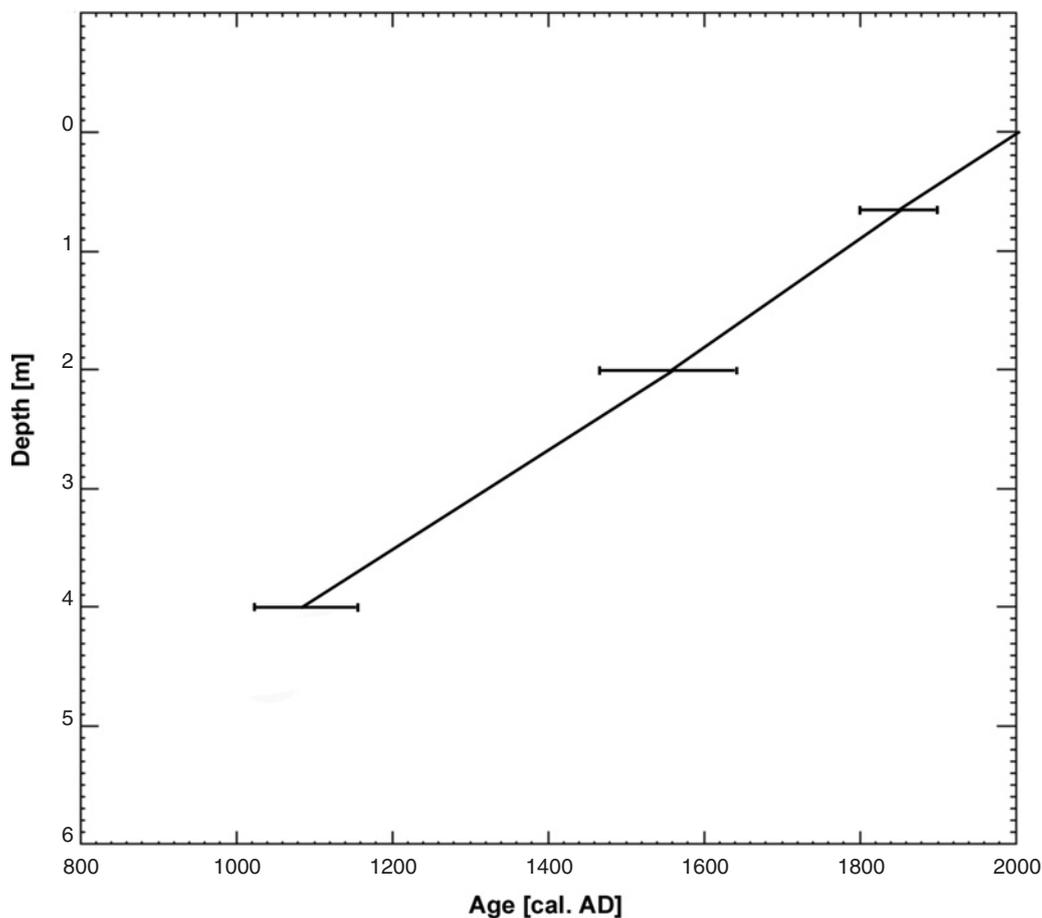
In EIG-2 (AD 1100–1350), TYPE EMA-104 shows very high and fluctuating values. *MONODICTYS* declines abruptly with the beginning of the zone but still plays an important role in the assemblage. The

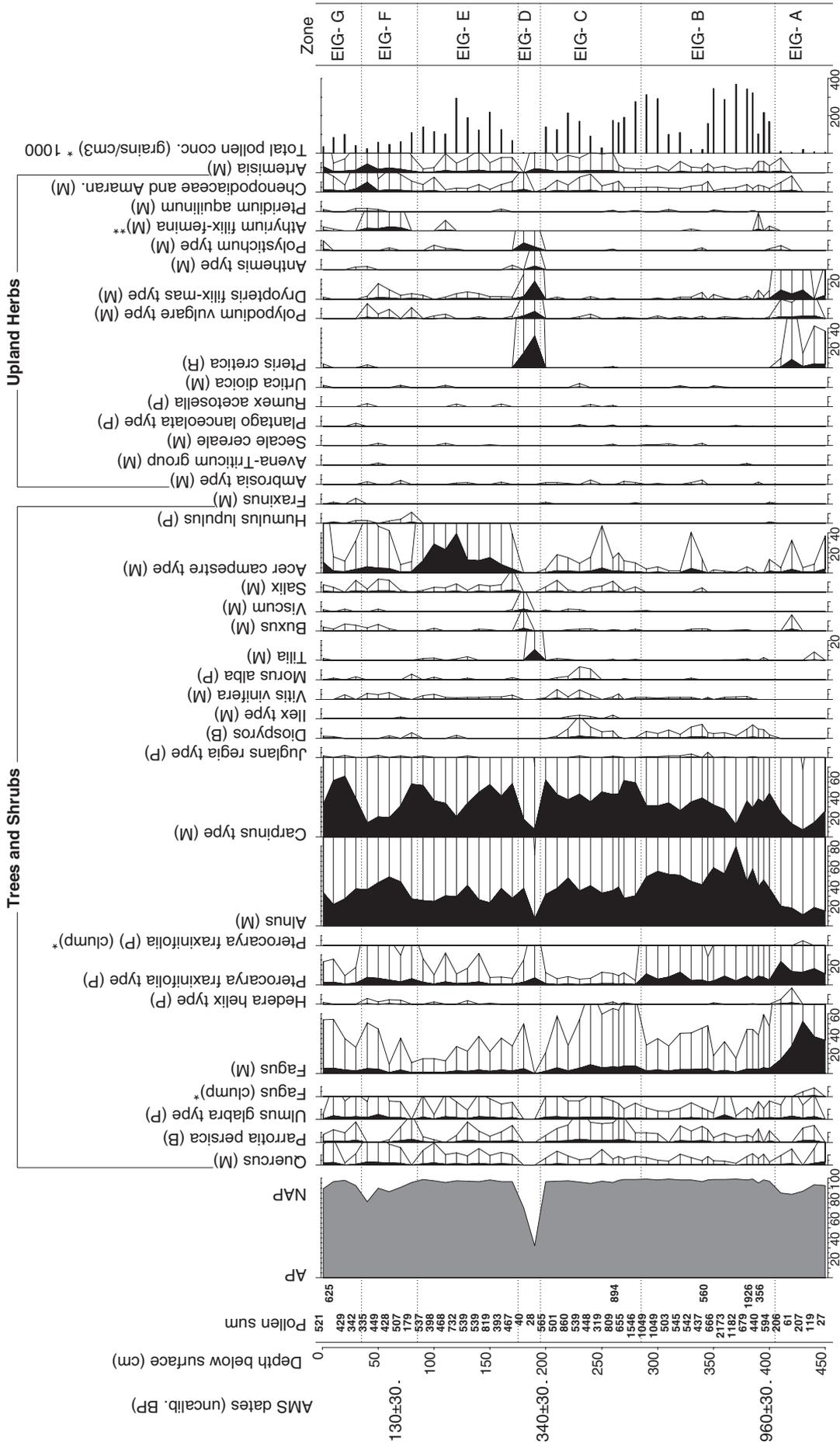
**Table 1** Depths, materials and results of the AMS  $^{14}\text{C}$  dates and calibrated ages from the EIG mire

$^{14}\text{C}$ lab. no.	Depth below surface (cm)	Dated material	AMS $^{14}\text{C}$ yr BP	Calibrated years AD (median value of 2 $\sigma$ ranges)
Poz-16796	68–70	<i>Alnus</i> nutlet, bicarpellate <i>Carex</i> fruit, cf. <i>Rubus fruticosus</i> seed, bud scales and tree leaf fragments of unknown origin	130 $\pm$ 30	1799–1893
Poz-16797	200–202.5	Tree leaf fragments of unknown origin	340 $\pm$ 30	1470–1639
Poz-16798	400–402.5	Bicarpellate <i>Carex</i> fruit, cf. <i>Rubus fruticosus</i> seed, <i>Ranunculus</i> fruit, tree leaf fragments and bud scales of unknown origin	960 $\pm$ 30	1021–1155

**Table 2** Lithostratigraphy of the EIG core

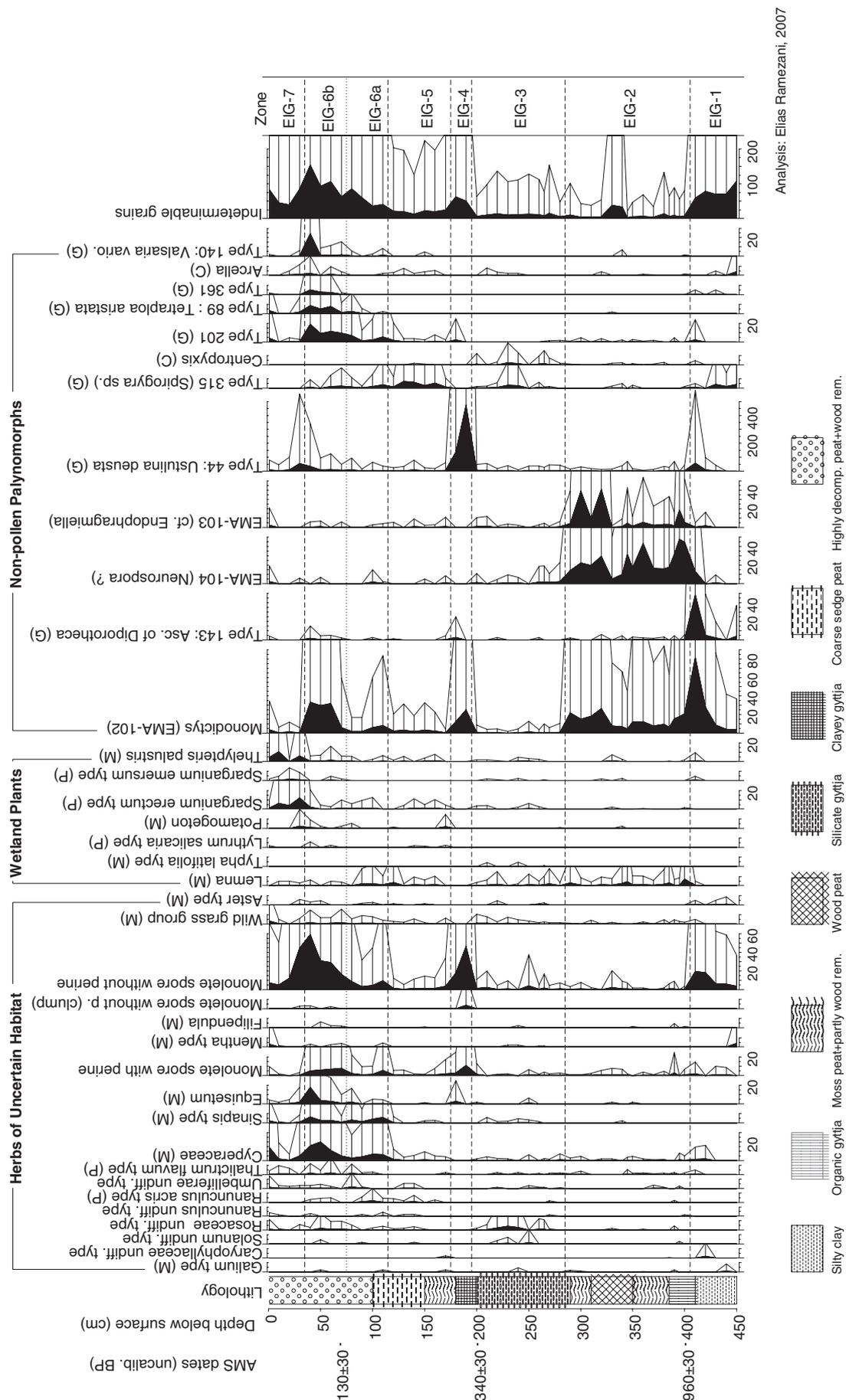
Depth below surface (cm)	Lithology
0–100	highly decomposed peat; partly wood remains; carbonate concretions in lower parts
100–150	coarse sedge peat; partly carbonate concretions
150–180	moss peat
180–200	clayey gyttja
200–290	silicate gyttja; less carbonate concretions than in deeper parts
290–310	moss peat; carbonate concretions
310–350	wood peat; carbonate concretions
350–385	moss peat; partly wood remains; carbonate concretions
385–410	organic gyttja; carbonate concretions
410–450	silty clay

**Figure 2** Age–depth model for the EIG mire, assuming constant sediment accumulation rates between the calibrated dates. Horizontal bars show the range of calibrated dates with a precision of 2  $\sigma$  ranges (for the youngest date, the median value of the 2  $\sigma$  ranges has been chosen)



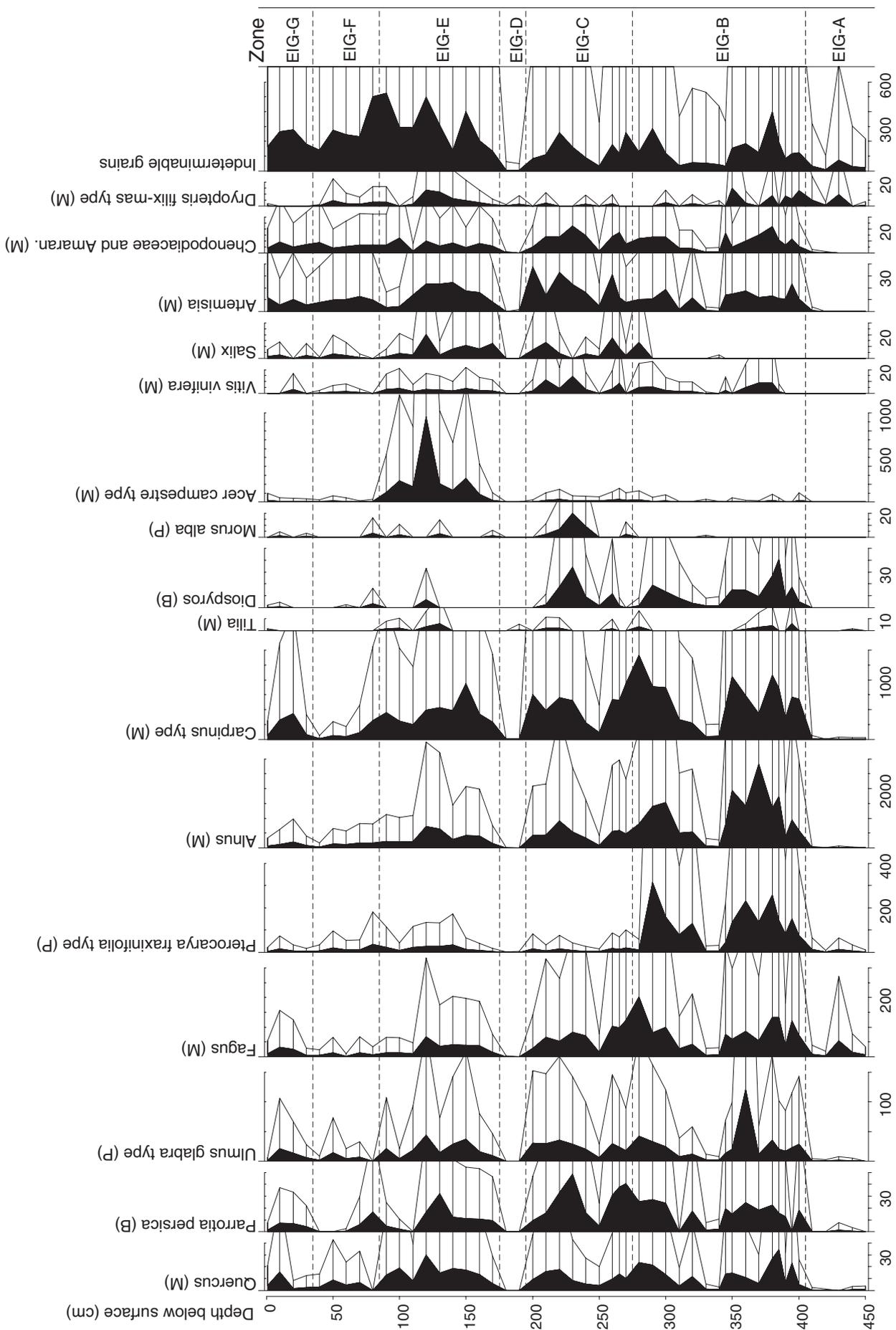
Analysis: Elias Ramezani, 2007

**Figure 3** Pollen percentage diagram of the EIG mire (arboreal and upland herb pollen). All the types are applied for the calculation of the pollen sum, except the clumps (marked with an asterisk). Relative pollen values are presented as percentages (closed curves) and a ten-times exaggeration (open curves with depth bars). The 'pollen sum' column displays the number of pollen included in the pollen sum. Pollen nomenclature follows Moore *et al.* (1991; epithet 'M' after the names of the types in the diagrams), Beug (2004; 'B'), Northwest European Pollen Flora ([AQ]P) and Reille (1992; 'R'). For detailed references see Materials and methods. For *ATHYRIUM FILIX-FEMINA* TYPE, see Appendix 2



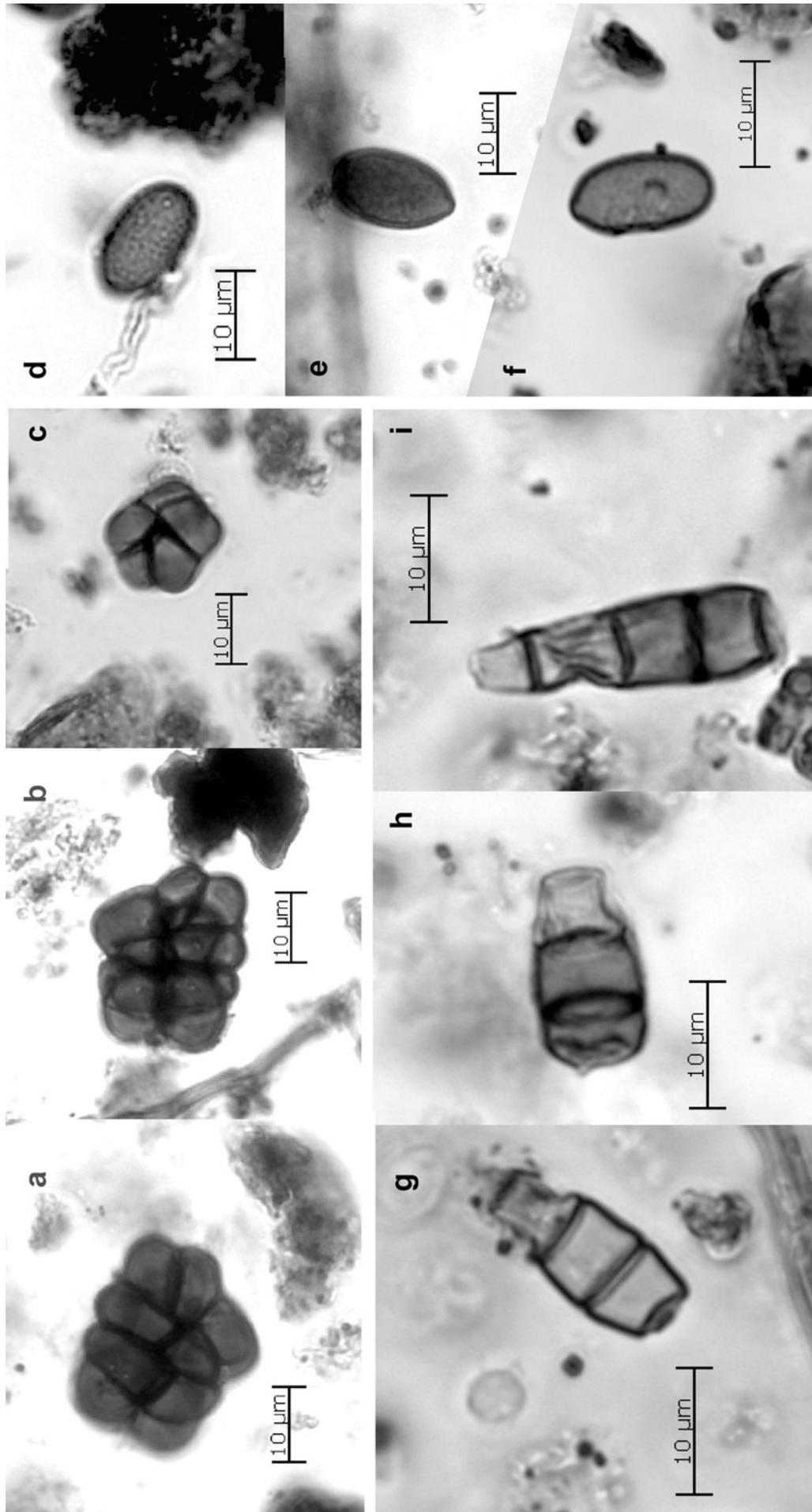
Analysis: Elias Ramezani, 2007

**Figure 4** Pollen percentage diagram of the EIG mire (wetland and ecologically undefined types = Types excluded from the pollen sum). Pollen and spore nomenclature follows Moore *et al.* (1991); epithet 'M' after the names of the types in the diagrams, 'B', Northwest European Pollen Flora ('P'), Reille (1992: 'R'), van Geel *et al.* ('G'), Ellis and Ellis (1997: 'E') and Charman *et al.* (2000: 'C'). For detailed references see Materials and methods. Identification of the new non-pollen palynomorphs (EMA-x; EMA = Ernst-Moritz-Arndt-University Greifswald) following André Aptroot (personal communication, 2007). The lithology of the core is presented at the left side of the diagram. For further description see Figure 3



Analysis: Elias Ramezani, 2007

Figure 5 Pollen concentration diagram of the EIG mire. Pollen concentration expressed in grains/cm³ per 100



**Figure 6** New non-pollen palynomorphs encountered in the EIG core. (a)–(c) Type EMA-102: Monodictys; (d)–(f) Type EMA-104: *Neurospora* (*Gelasinospora*-type) (?); (g)–(i) Type EMA-103: *Endophragmiella* (?). For further explanation see Appendix 3

**Table 3** Overview of palaeoecological events in and around the EIG site

Zone	Date in yr AD	Wetland	Extralocal upland 550 m a.s.l.	Higher mountains >550 m a.s.l.	Caspian lowlands ± 0 m a.s.l.	Historical sources	Over-regional climate	
							EIG signal	Bradley <i>et al.</i> (2003a, b) (B); Stevens <i>et al.</i> (2006) (S), Touchan <i>et al.</i> (2007) (T)
EIG-A	Before 1088	Wet basin with clay sedimentation	<i>Pterocarya</i> forest	Erosion of forest soil in <i>Fagus</i> zone	Hardly any cultural indicators	Human habitation in Chalus (cf. Figure 1)	Erosion probably by heavy rainfall	'Mediaeval Climatic Anomaly' (heavy rainfall?) (B, T)
EIG-B	1088– 1350	Lake with deposition of organic gyttja	<i>Pterocarya</i> forest		Some cultural indicators	Human habitation in Chalus		
EIG-C	1350– 1560	Lake with sedimentation of clastic material	Some human use of forest		Increased cultural indicators	Human habitation in Chalus	Warmer and/or drier conditions?	Dry interval at 500 cal. year BP (S)
EIG-D	1560– 1600	Lake with rapid clay sedimentation	Rapid clay deposition	Land slide/ erosion	Cultural indicators	Human habitation in Chalus	Heavy rainfall event	Onset of 'Little Ice Age' (B), wet years (T)
EIG-E	1600– 1800	Wet open sedge fen	Open pioneer vegetation of <i>Acer</i>		Cultural indicators	Human habitation in Chalus		'Little Ice Age' (B), drier climate (T)
EIG-F	1800– 1940	Drier open sedge fen	Forest recovery and renewed opening		Most cultural indicators	Human habitation in Chalus, first presence in Nowshahr area		
EIG-G	Since 1940	Shaded, wet eutrophic fen	Re- establishment of closed forest		Cultural indicators	Rapid expansion of Nowshahr and Chalus		Recent warming (B)

upper half of the zone is characterized by increased values of TYPE EMA-103, a fungal spore that probably can be ascribed to *Endophragmiella* (André Aptroot, personal communication, 2007; Figure 6g–i; Appendix 3). This Hyphomycete comprises many species that grow on rotten wood of several tree species (Ellis and Ellis, 1997). LEMNA is also prominent. CYPERACEAE, WILD GRASS GROUP and THALICTRUM FLAVUM TYPE are frequently present with low values. With the exception of a small peak in the central part of the zone, indeterminable grains show relatively low values. The deposits of this section consist both of gyttja and of moss and wood peat. Calcium carbonate concretions are common throughout the deposit.

EIG-3 (AD 1350–1560) is characterized by dramatic declines of TYPE EMA-104, MONODICTYS and TYPE EMA-103 (ENDOPHRAGMIELLA?). Here LEMNA occurs with lower values, whereas ROSACEAE UNDIFF., CENTROPYXIS and SPIROGYRA exhibit higher values than before. The sediment is composed predominantly of silicate gyttja, with carbonate concretions in the lower part but noticeably lessening in the upper part of the zone.

EIG-4 (AD 1560–1600) is primarily characterized by the peaks of MONODICTYS, MONOLETE SPORES and USTULINA DEUSTA, which, as mentioned in zone EIG-D, may reflect the inwashed soil from a *Pterocarya* forest (see also zone EIG-A).

In EIG-5 (AD 1600–1710) TYPE 315 (SPIROGYRA) attains its highest values through the whole record. The lithological change of moss peat into coarse sedge peat within this zone may indicate the further terrestrialization of the basin. Carbonate precipitation is common in most parts of the zone.

EIG-6 (AD 1710–1940) has been subdivided into two subzones. EIG-6a (AD 1710–1830) shows slightly increased values of MONOLETE SPORES, CYPERACEAE, EQUISETUM, SINAPIS, WILD GRASS GROUP, MONODICTYS, TYPE 201, TETRAPLOA ARISTATA (TYPE 89) and VALSARIA VARIOSPORA (TYPE 140); while in EIG-6b (AD 1830–1940) these types show substantially higher values. These high values, together with an increase in the amount of indeterminable grains, correlate very well with human interference, which has the maximum extent of the whole record in this zone,

particularly in EIG-6b. The deposit mainly consists of highly decomposed peat with some rather large wood remains.

In EIG-7 (since AD 1940) SPARGANIUM ERECTUM and THELYPTERIS PALUSTRIS comprise the most prominent wetland types. Values of CYPERACEAE and indeterminate grains are much lower than in the previous zone but, like SINAPIS, WILD GRASS GROUP and TETRAPLOA ARISTATA, they increase near the surface of the mire. POTAMOGETON has a small peak at the beginning of the zone. Like the previous zone, the deposit consists of highly decomposed peat with wood remains.

## Discussion and conclusions

The record starts with an erosional event (Zone EIG-A, before AD 1100) that falls in the 'Medieval Climatic Anomaly', a period with significantly higher temperature and prolonged droughts in some areas and exceptional rains in others (Bradley *et al.*, 2003a, b). Also the tree ring data of Touchan *et al.* (2007) suggest a concentration of wet years in southwestern Anatolia in the eleventh century. Furthermore, the formation of the basin, probably as a result of karst, is an indication of radical hydrological changes during that period.

After having been an important element in the forest from before AD 1100 *Pterocarya* dramatically declines around AD 1350, an event that points to warmer and/or drier conditions. A similar prevalence of *Pterocarya (fraxinifolia)* around 1000 cal. yr BP followed by a decline some centuries later has been shown for the Ispani area of Colchis (western Georgia) (cf. Connor *et al.*, 2007; Pim de Klerk, personal communication, 2007) and may reflect a regional climatic phenomenon. The inferred drier climatic conditions correspond in timing fairly well to the dry interval at 500 cal. yr BP suggested by Stevens *et al.* (2006) on the basis of oxygen-isotope analysis at Lake Mirabad in western Iran (cf. Figure 1)

Our data reveal that human impact has affected the forests in the study area since at least AD 1100, when sediment deposition in the EIG basin started (Table 3). This corresponds to archaeological finds of wood-cutting for metal smelting in the central Caspian forests since at least 1500–2000 BC (Dr Seyed Mehdi Mousavi, Tarbiat Modarres University, Iran, personal communication, 2007) and to historical records that provide evidence that human habitation in the Caspian coastal areas in Chalus (Figure 1) is older (possibly several centuries) than the time span covered by the EIG core (Mahjoori, 2002). To what extent the erosional event of Zone EIG-A (before AD 1100) is attributable to human intervention or has a climatic background (or a combination of both) is open to debate. The zone does not contain anthropogenic indicators except in its upper part.

The extent and intensity of early human interference with the forest composition and structure are not yet clear but could have been important, as the presence of DIOSPYROS and JUGLANS in zone EIG-B suggests. Our data further indicate that human influence in the central Caspian forest increased noticeably in the fifteenth and sixteenth century. This may have culminated in a second erosional event around AD 1560–1600 (cf. EIG-D), which also may have been related to climate, ie, the beginning of the 'Little Ice Age' (cf. Bradley *et al.*, 2003a). European climate showed a significant shift towards cooler and more humid conditions in the second half of the sixteenth century with substantially more storms and floods (Pfister and Brázdil, 1999). Also Touchan *et al.* (2007) found the years AD 1518 to 1587 to be the most humid period in southwestern Anatolia in the past 900 years.

After this supposed landslide a pioneer forest dominated by *Acer* was established that was replaced by a more diverse forest in the subsequent 400 years.

Since AD 1800, the reconstructed sharp decline of *Carpinus* and *Parrotia persica* reflects the effects of charcoal production, which was widespread from the 1850s until around 1960 (Ehlers, 1996–2007a). Similar broad-scale human impacts have been described for the lowlands of Colchis, where forest cover was largely destroyed and replaced with plantations of tea, citrus, etc. in the twentieth century (Connor *et al.*, 2007; Pim de Klerk, personal communication, 2007). The opening of the forest canopy also led to vegetational changes in the EIG mire basin itself, where sedge fen species expanded. After 1940 a closed forest was re-established.

This picture of early human interference concurs with the opinion of Zohary (1963) that the composition of the Caspian forests has been altered significantly through time. It contradicts the common view that the Caspian forest belt had remained more or less untouched until the end of the nineteenth and the beginning of the twentieth century (cf. Ehlers, 1996–2007a). In spite of human interventions, however, the landscape directly surrounding the EIG mire has always been a species-rich, broadleaved forest during the past millennium, illustrating the long-term continuity of forest cover in that area.

## Acknowledgements

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## Appendix 1: pollen/spore types not shown in the pollen diagrams

400(0.2) = 400 cm 0.2%

### A. Pollen sum types

#### Trees and shrubs

BETULA (M): 80(1.7), 130(0.2), 170(0.4), 290(0.1), 395(0.6);  
 CELTIS(M): 395(0.3); FRANGULA ALNUS (M): 70(0.4), 280(0.1),  
 400(0.2); JUGLANS REGIA /PTEROCARYA FRAXINIFOLIA: 320(0.2),  
 330(0.2), 370(0.1), 400(0.2); MORUS ALBA TYPE (P): 265(0.1); POPULUS  
 (M): 100(0.3), 210(0.2), 230(0.2), 250(0.3), 330(0.2); PTEROCARYA  
 FRAXINIFOLIA/CARPINUS TYPE: 10(0.3), 30(0.3), 40(0.6), 60(0.7),  
 70(1.2), 110(0.2), 160(0.5), 180(2.5), 260(0.4), 270(0.2), 330(0.4),  
 340(0.5), 380(0.1), 400(0.2), 410(0.5), 430(1); TAXUS (M): 260(0.4).

### Upland herbs

ASTRANTIA MAJOR (P): 400(0.2); BUNIUM BULBOCASTANUM (P): 250(0.3); BUPLEURUM FALCATUM GROUP (P): 10(0.6), 30(0.6), 370(0.1); CAMPANULA (M): 260(0.1); CICHORIM INTYBUS TYPE (M): 340(0.2); ERYNGIUM CAMPESTRE TYPE (P): 160(0.3), 170(0.2); EUPHORBIA (M): 210(0.2), 350(0.2), 380(0.1); GERANIUM PRATENSE GROUP (P): 250(0.3); GLAUCIUM FLAVUM TYPE (M): 210(0.2); GYPSOPHILA REPENS TYPE (M): 30(0.3); JASIONE TYPE (M): 260(0.1), 265(0.1); MONOTROPA (M): 60(0.2); PARIETARIA (M): 400 (0.2); PIMPINELLA ANISUM TYPE (P): 1(0.2), 10(0.2), 60(0.2), 220(0.2), 230(0.4); PIMPINELLA MAJOR TYPE (P): 130(0.2); PLANTAGO CORONOPUS (M): 340(0.2); POLYGONUM AVICULARE TYPE (P): 280(0.1); RANUNCULUS ARVENSIS TYPE (P): 60(0.5); SANICULA EUROPAEA (P): 50(0.2), 70(0.2); SCABIOSA (M): 260(0.1); SECALE CEREALE/AVENA-TRITICUM GROUP (M): 390(0.2); TORILIS ARVENSIS (P): 260(0.1); TORILIS NODOSA TYPE (P): 230(0.4); TRINIA GLAUCA TYPE (P): 260(0.2).

### B. Types excluded from the sum

#### Trees and shrubs

ALNUS (M) clumps: 370(0.2), 430(0.5); CARPINUS TYPE (M) clumps: 380(0.1); HIPPOPHAE RHAMNOIDES (M): 90(0.2); cf. PLATYCARYA (B): 395(0.3); PINUS (M): 120(0.1).

#### Herbs

ALCHEMILLA TYPE (M): 385(0.1); APIUM INUNDATUM TYPE (P): 100(0.3), 150(0.1); CIRSIUM (M): 70(0.2); cf. DRYOPTERIS DILATATA (M): 50(0.2); GEUM (M): 50(0.2), 210(0.6); HORDEUM GROUP (M): 1(0.2), 70(0.2), 280(0.1), 360(0.05); HYDROCOTYLE VULGARIS (M): 265(0.1); LACTUCEAE UNDIFF. TYPE: 60(0.5), 410(0.5); LOTUS (M): 60(0.2); PLANTAGO UNDIFF. TYPE: 400(0.2); POACEAE UNDIFF. TYPE: 340(0.2); POLYGONUM PERSICARIA TYPE (P): 1(0.2), 40(0.3); POTENTILLA (M): 50(0.4), 60(0.5), 110(0.2), 260(0.9); RUMEX ACETOSA TYPE (P): 40(0.6); R. AQUATICUS GROUP (P): 360 (0.1); cf. SAXIFRAGA OPPOSITIFOLIA TYPE (P): 100(0.8), 110(0.2), 120(0.1), 130(0.2), 140(0.2), 150(0.2); cf. SAXIFRAGA STELLARIS TYPE (P): 1(0.2), 50(0.2), 60(0.7), 220(0.1), 385(0.1); SCROPHULARIA TYPE (M): 50(0.2), 220(0.1), 290(0.1); STACHYS SYLVATICA TYPE (M): 50(0.2), 60(0.2); THALICTRUM FLAVUM GROUP (P): 10(0.2), 100(0.3), 210(0.2).

#### Aquatic and wetland plants

MYRIOPHYLLUM SPICATUM TYPE (P): 60(0.2), 250(0.3), 280(0.1), 345(0.2), 385(0.05); PRIMULA FARINOSA-TYP (B): 205(0.3); TYPHA ANGUSTIFOLIA (P): 110(0.2).

#### Non-pollen palynomorphs

ONCOPODIELLA (E): 60(0.2), 310(0.4), 320(0.6), 330(0.2), 385(0.2); SILLIA FERROGINEA (E): 1(0.4), 40(0.3), 110(0.2); SPORE TYPE D (SPIROGYRA SP.) (G): 60(0.2), 230(0.9); TYPE 128 (G): 1(0.4), 20(0.2), 30(0.3), 40(0.6), 50(0.2), 60(0.7), 90(0.2); TYPE 140 (clumps): 40 (3.2); TYPE 361 (clumps): 40(1.2), 60(0.5).

## Appendix 2: pollen and spore types not described in the literature

JUGLANS REGIA/PTEROCARYA FRAXINIFOLIA, PTEROCARYA FRAXINIFOLIA/CARPINUS and SECALE CEREALE/AVENA-TRITICUM GROUP refer to grains that, due to folding, corrosion or concealment, could not be attributed to JUGLANS REGIA, PTEROCARYA FRAXINIFOLIA, CARPINUS, SECALE CEREALE or AVENA-TRITICUM GROUP, respectively.

MONOLETE SPORE WITHOUT PERINE refers to all psilate monolete spores. MONOLETE SPORE WITH PERINE includes all monolete spores with perine that were not further identified. ATHYRIUM FILIX-FEMINA TYPE (marked with two asterisks in Figure 3) was determined only

from the middle of the counting procedure; hence its values are also included in MONOLETE SPORES WITH PERINE TYPE.

The CARYOPHYLLACEAE UNDIFF., ROSACEAE UNDIFF., UMBELLIFERAE UNDIFF., LACTUCEAE UNDIFF. and SOLANUM UNDIFF. include all grains that show marked morphological similarity with most pollen types produced by Caryophyllaceae (cf. Punt *et al.*, 1995), Rosaceae (cf. Moore *et al.*, 1991), Umbelliferae (cf. Punt and Clarke, 1984), Lactuceae (cf. Moore *et al.*, 1991) and Solanum (cf. Moore *et al.*, 1991) taxa, respectively, but that were not further identified.

## Appendix 3: short description of the new non-pollen palynomorphs recorded in this paper

TYPE EMA-102: MONODICTYS (Figure 6a–c): multicelled conidium, subspherical (to spherical) and lobed, (15)20–30(35) µm in diameter, 10–15 or even more single cells; single cells also globose to somewhat elliptical and 6–10 × 6–13 µm (rarely smaller conidia with only 5–6 cells are observed), each septum with pore, whole conidium middle to dark brown and psilate. According to André Aptroot (personal communication, 2007) this type consists of the conidia of the Hyphomycete *Monodictys*.

TYPE EMA-103 (Figure 6g–i): conidium, ovoid elongated to almost cylindrical, 3-septate, 14–15 × 7–9 µm, sometimes with remnant of conidiophore (then the total length: up to 24 µm), both central cells hyaline to pale brown and wall thicker than in end cells, apical end cell rounded, sometimes pointed and crinkled or even detached, proximal end cell slightly tapering and truncate with large aperture (hilum?). This is probably an *Endophragmiella*, a Hyphomycete (André Aptroot, personal communication, 2007).

TYPE EMA-104 (Figure 6d–f): fungal spore, elliptical to ovoid, 14–15(17) × 8–9 µm, surface covered with small pits resembling a microreticulum with thick walls and small lumina, yellowish brown, one end with slightly protruding pore of 0.7 µm in diameter, sometimes pore not at the very top of the spore but somewhat lateral displaced. This fungal spore can possibly be ascribed to the Ascomycete *Neurospora* (GELASINOSPORA-TYPE) (André Aptroot, personal communication, 2007).

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