

APIACEAE – CONTRIBUTION TO THE FLORA HISTORY IN LIGHT OF POLLEN ANALYSIS WITH A SPECIAL REFERENCE TO THE HOLOCENE SITE AT BŁĘDOWO (CENTRAL POLAND)

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Abstract

Pollen grains of Apiaceae from the profile at Błędowo, Mazovia region, Central Poland were identified. Pollen of this family occurs in higher frequencies in the Late Glacial, the beginning of the Holocene and in the periods under strong human influence. Transfer of pollen of Apiaceae from plants to lake deposits is different for particular species and depends rather on insect activity during the season as well as on the activity of their predators and/or the oscillation of animal populations than the selectivity in insect feeding. Different environmental conditions around the sites, which result in various patterns of transfer agents can cause some difficulties in interpretation of vegetational changes inferred from pollen data.

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Key words: Apiaceae, pollen, Holocene, Syrphidae, Pleistocene

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INTRODUCTION

Pollen of Apiaceae is a relatively rare guest in palynological sections as it is produced by insect pollinated plants. However, in some parts of pollen diagrams these grains are more common. Their identification, despite the availability of excellent key (Punt 1984) is not an easy task not only because of great similarities of pollen types but mainly because of variation in pollen morphology even within one inflorescence. *Bupleurum*, *Pleurospermum*, *Heracleum*, *Oenanthe*, *Cicuta* or *Pimpinella* are the most often identified pollen types, relatively easy to determine. However also this rather well distinguishable pollen may cause problems and false diagnoses. Pollen of the last two taxa is characterized by great variation of shape and exine morphology. *Pleurospermum austriacum* known from Pleistocene sections is similar to some degree with the occurring in Poland *Ligusticum mutellina* and *Meum athamanticum*.

It seems that pollen of insect pollinated plants (including Apiaceae) are transferred to sediments after consumption by animals, especially insects, eating pollen and nectar, sometimes even the entire inflorescences (e.g. well known larvae of Lepidoptera – *Papilio machaon*). Their faeces can be deposited directly into the basin, or through participation of predators (e.g. swallows), in excrements of which the author found numerous types of Apiaceae pollen occurring in the study area, which prove such kind of pollen source in sediments.

The aim of this study is to determine the character and dynamics of the Apiaceae occurrence mainly in the Late Gla-

cial and the Holocene sediments based primarily on specimens collected from the earlier examined Błędowo site (Bińka *et al.* 1991, Fig. 1), as well as the factors determining taxonomic composition and fluctuations of pollen content. In this analysis it is important to trace the route of Apiaceae pollen, initially consumed by insects and next transported by predators until it finally reaches sediments as well as to answer the question whether such consumption of Apiaceae pollen is of selective character as an effect of differences in feeding preferences and whether it can result in some selectivity in further pollen transfer.

It is obvious that only a very narrow fragment of the possible routes of entomophilous pollen can be traced, because the full list of their consumers is very long. As hoverflies are considered the main pollen feeders, the feeding preferences of most common species of this insect group, observed and caught on flowers of the Apiaceae, were analysed. The other routes of this pollen dispersal are not a matter of debate in this study due to the difficulties with collecting the full range of faeces of higher animals e.g. Odonata, birds or bats. Nevertheless, selected aspects affecting such transfer e.g. fluctuations in their population level and the influence of size of the foraging area on the pollen deposition are discussed.

A general question arises as to what degree the fluctuations of pollen curves of insect pollinated plants reflect (or do not) the changes of their contribution in plant communities and whether this pattern is a result of some persistent balance between the transfer agents. In other words the increase of importance of such species in the area surrounding the basin may not correspond to the rise of pollen curves in the dia-



Fig. 1. Sites mentioned in the text: 1. Błędowo, 2. Warsaw, 3. Góra Kalwaria, 4. Mordy, 5. Białogóra, 6. Świnna Poręba, 7. Kalińów, 8. Zakrzze, 9. Woskrzenice, 10. Dzięwule, 11. Nakło, 12. Ossówka, 13. Gościąg, 14. Żarnowiec, 15. Nidzica, 16. Wolin, 17. Kraków, 18. Przemyśl, 19. Czernsk, 20. Mielnik, 21. Olsztyn n. Częstochowa, 22. Zbójno.

gram, also the lack or limitations in the transfer agents of higher rank (a fact which is not hard to imagine), will result in the relative absence (or small content) of pollen of these plants in deposits despite their presence in the area. The issue is whether it is possible to make comparisons between sites, taking into account the content of entomophilous pollen and if it is possible to draw any environmental conclusions based on this kind of data.

MATERIAL AND METHODS

Collection of the reference material and identification of Apiaceae pollen

Reference material for Apiaceae pollen was removed from plants growing mostly in Mazovia Lowland, Podlasie region and Holy Cross Mts. In many cases several samples from hermaphrodite and male flowers and from the primary, secondary and tertiary umbels of the individual plants were picked up.

Fossil pollen was identified using reference collection for Apiaceae, the available keys (e.g. Punt 1984) and photographs, as well as on the basis of the author's own observation of the morphological features especially of these species outside the range of "The Northwest European Pollen Flora".

Faeces collection and laboratory procedures

The sampling area (Fig. 1) included Warsaw (Ochota, Służewiec and Powsin districts) with high level of anthropopressure, the vicinity of Góra Kalwaria (a typical rural environment), Błędowo (the transitional area between lake and cropland), Mazovia region, the vicinity of Mordy (croplands,

meadows), Podlasie region and Białogóra near Łeba, Pomorania (marginal forest zone and open areas). The full list of Apiaceae species, on which syrphids were observed and caught is as follow: *Berula erecta*, *Pastinaca sativa*, *Cicuta virosa*, *Anthriscus sylvestris*, *Aethusa cynapium*, *Daucus carota*, *Carum carvi*, *Angelica sylvestris*, *Angelica archangelica*, *Aegopodium podagraria*, *Eryngium planum*, *Libanotis pyrenaica*, *Sium latifolium*, *Peucedanum oreoselinum*, *Torilis japonica*, *Chaerophyllum temulum*, *Ch. aromaticum*, *Ch. bulbosum*, *Heracleum sibiricum*, *H. sphondylium*, *Osterticum palustre*, *Pimpinella saxifraga* and *Selinum carvifolia*. Hoverflies were collected at different intervals during the period from 9th Mai to 10th September. They were collected at sunny days between 10.00 and 15.00. The insects were held in closed traps for over 20 hours (a few drops of water were added to each bottle), and after that time anaesthetized with CO₂. Faeces was transferred into polypropylene test-tube and treated with standard procedure (acetolyse) using *Lycopodium* tablets as a marker to estimate the pollen concentration in the faeces.

Pollen from faeces was identified to the type or, if possible, to a species level. Syrphids were identified using among others a detailed key of Bańkowska (1963) and keys to some genera (Veen van M. unpubl.).

RESULTS

Variation in size and shape of Apiaceae pollen

Variation in pollen size in Apiaceae is considerable. According to some authors this variation depends on the floral type e.g. whether pollen are collected from unisexual (male) or hermaphrodite (staminate and pistillate) flowers (McKone and Webb 1988). Andromonoecious, mostly protogynous species bearing flowers of two types – hermaphrodite and male – are very common in Apiaceae. A distribution pattern of these flowers in individual plants and even in single compound umbels is different in particular species of Apiaceae and may vary in the population depending on local habitat condition (Knuth 1898). Van der Pluym and Hideux (1977) observed that the size and to some degree also the shape of pollen of *Eryngium maritimum* varied in individual plants according to the type of inflorescence (primary, secondary and tertiary), and related this variation to the different nutrient supply.

Variation in pollen shape observed in insect faeces and fossil samples is still more astounding. Most often, a shortening of the long axis is observed. Also in pollen types with typically "curved or straight inner contour" (using Punt's terminology) a straight or distinctly convex contour is sometimes noted in the same species. Therefore sometimes some grains in reference slides resemble those of *Bupleurum* type in outline. These variations are well illustrated in the atlas of pollen of Europe and North Africa (Reille 1992). *Pastinaca sativa*, *Torilis nodosa*, *Cicuta virosa* and *Selinum carvifolia* pollen grains are the best examples of such variation in shape.

Pollen spectra from insect faeces

The state of pollen preservation after passing through insect guts was very good. Cracked pollen or broken ridges in

Compositae Liguliflorae pollen were sometimes observed. Only sporadically grains of Apiaceae were found in half. Signs of pseudogermination (Bińka 2003) were observed *e.g.* in faeces of *Episyrphus balteatus* feeding on *Cicuta virosa*. No evidence of endexine destruction was found.

A total of 183 hoverflies (16 species) feeding on Apiaceae were analyzed in respect to pollen content in faeces (Figs 2–6). Most of them are very common species of almost all habitats (Bańkowska, 1980, 1981). In addition, dietary needs of 63 individuals visiting other plants were identified. Faeces of 121 of 183 investigated hoverflies contained pollen of such species of Apiaceae on which they were caught (Tab. 1). Pollen of insect pollinated plants almost exclusively predominated in the guts. Anemophilous pollen was found only in taxa with reported preference to such pollen *e.g.* *Melanostoma* and *Platycheirus* (Goot, Graband 1970, Ssymank, Gilbert 1993). The small content of that group in the analysed samples arises from their low activity at the time of the day when other hoverflies were picked up.

Among insect species represented by statistically more reliable sample (*E. arbustorum* – Fig. 2, *M. florea* – Fig. 3, *S. pipiens* – Fig. 4, *S. stricta* – Fig. 5) individual males, on average, consumed considerably less pollen and less diversified as concerns pollen types than females (Tab. 1). These results are in accordance with conclusions of Haslett (1989) and Hickman *et al.* (1995) that male flies of the same species are more selective and eat less pollen than female ones. The number of pollen types in most examined samples oscillates between 2 and 3 (maximum 6). Diagrams of pollen consumption show that the number of pollen in the faeces is very diversified (even within the same species) and depends mostly on the insect size. Small syrphids such as *Sphaerophoria scripta* and *Syrretta pipiens* excreted faeces with small portion of pollen whereas bigger ones – *e.g.* *Eristalis* or *Myiatropa* – have in excrements even up to 3,000,000 pollen in the gut (maximum values – females of *Eristalis arbustorum* – 3,089,000, 1,299,000 and 1,134,000, male of *E. tenax* – 1,093,000, female of *E. nemorum* – 1,653,000), the values not yet reported from the hoverflies guts. In most cases the number oscillates between few thousands and several hundred thousands grains per one insect gut. The latter number agrees partially – when we exclude maximum values – with other estimations where different laboratory methods of pollen collection were used (Hickmann *et al.* 1995, Dlussky, Lavrova 2001).

Plant species that were especially attractive to investigated species of syrphids include members of Apiaceae, Compositae (*Anthemis* type – found in 103 of 246 faeces, Compositae Liguliflorae and other types), and Cruciferae (in 92 of 246). This pattern partly reflects entomophilous plant composition in open areas.

Adults of hoverflies generally display in part some pollen preferences. Some taxa feed on anemophilous pollen, however, in faeces of most species a broad range of entomophilous types can be found. Haslett (1989) showed that some syrphids species exhibit a high degree of selectivity and the others forage for pollen of numerous plant species. Hoverflies feeding on Apiaceae flowers show some selectivity in their dietary needs in relation to the whole family. *Myiatropa*, in comparison with other syrphids, seems to prefer

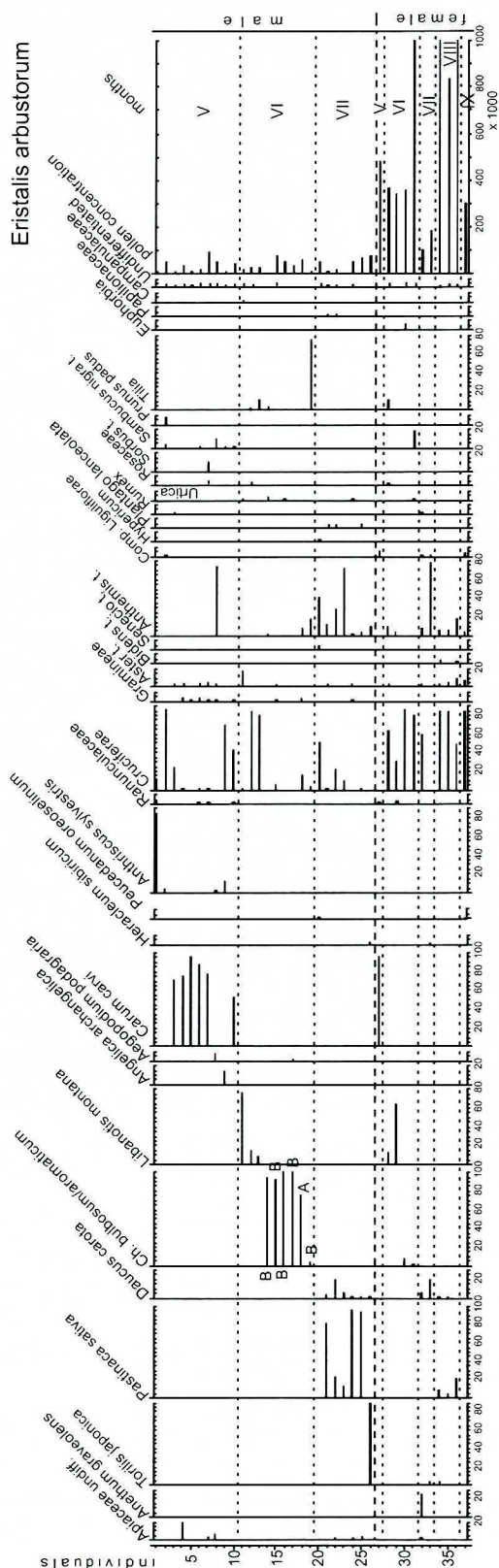


Fig. 2. Histogram showing the pollen content in the faeces of 37 individuals of *Eristalis arbustorum* visiting flowers of Apiaceae members (L.), male (m) 1–26, female (f) 27–37. The letter A marks individuals observed and caught on *Ch. aromaticum*, the letter B – on *Ch. bulbosum*.

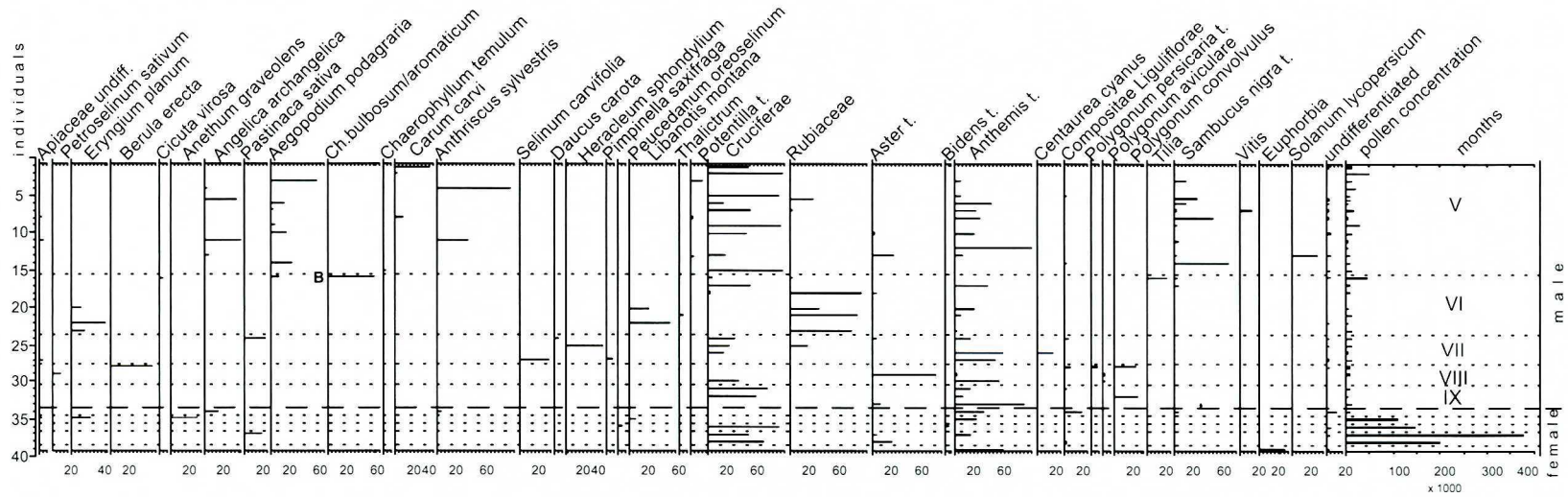


Fig. 4. Histogram showing the pollen content in the faeces of 39 individuals of *Syritta pipiens* (L.), (m) 1–33, (f) 34–39.

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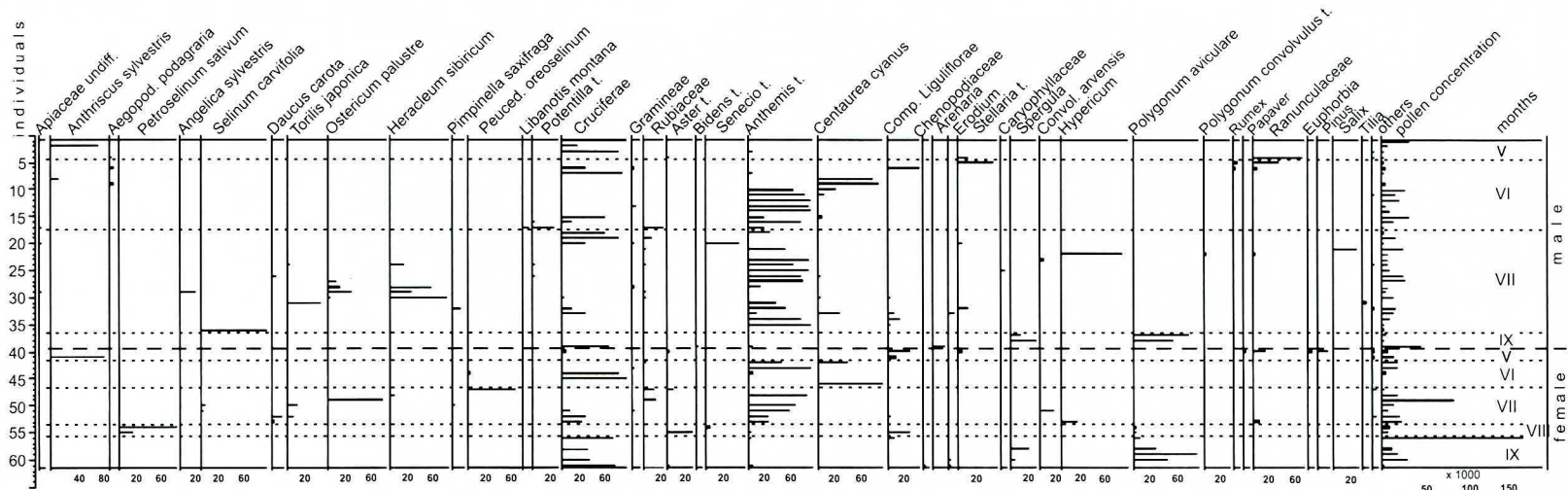


Fig. 5. Histogram showing the pollen content in the faeces of 61 individuals of *Sphaerophoria scripta* (L.), (m) 1–39, (f) 40–61.

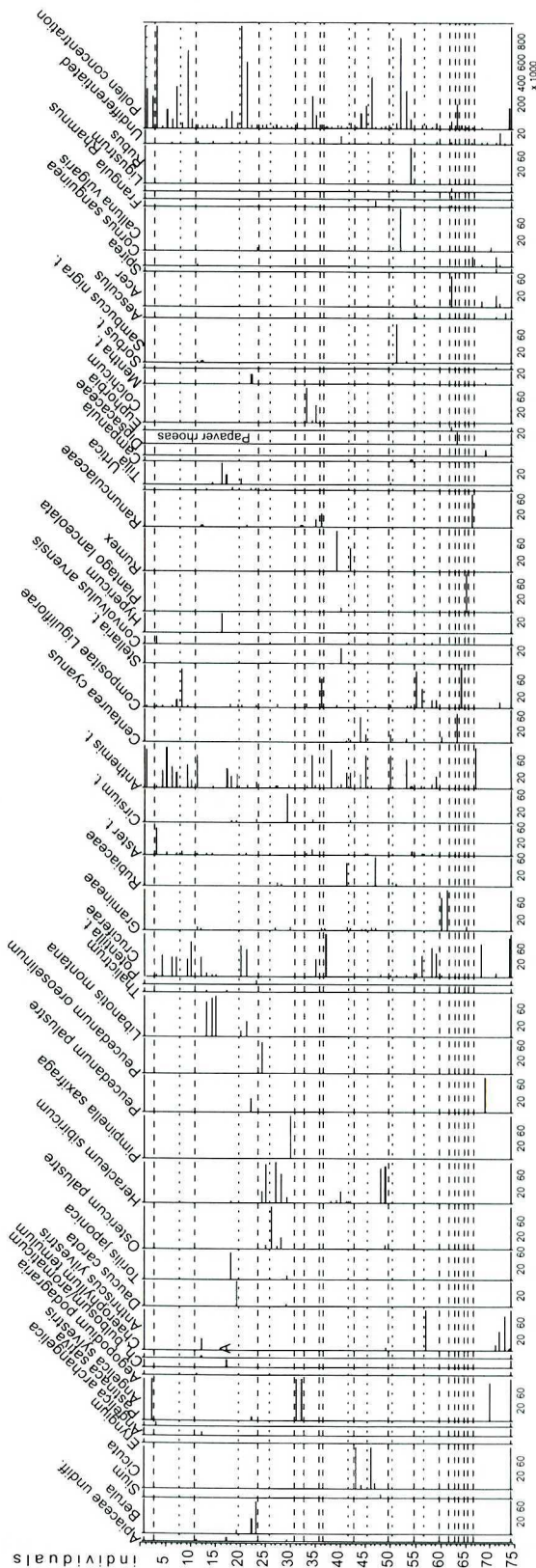


Fig. 6. Histogram showing the pollen content in the faeces of individuals of *Eristalis pertinax* (Scop.) (m) 1, (f) 2; *Eristalis tenax* (L.) (m) 3-7, (f) 8-10; *Eristalis nemorum* (L.) (m) 11-19, (f) 20-23; *Syrphus vitripennis* Meig., (m) 24-25, (f) 26-30; *Melangyna umbellatarum* (Fabricius, 1794) (f) 31-32; *Syrphus ribesii* (L.) (f) 33-35; *Eupeodes luniger* (Meigen, 1822), (m) 36; *Eupeodes collariae* (Fabricius, 1794), (m) 37-41, (f) 42; *Episyrphus balteatus* (De Geer, 1776), (m) 43-45, (f) 46-49; *Helophilus pendulus* (L.) (m) 50, (f) 51-54; *H. trivittatus* (Fabr.) (m) 55-56, (f) 57-59; *Melanostoma melinum* (L.) (f) 60, (m) 61; *Chrysotoxum vernalis* Loew, (f) 62; *Chrysotoxum cautum* (Harr.) (f) 63; *Neoscasia podagrica* (Fabr.) 64; *Platycheirus chypeatus* (Meig.), (m) 65; *Xanthogramma ornatum* (Meig.), (f) 66; Insecta undiff. 67-74.

Apiaceae pollen (especially *Pastinaca sativa*) and it uses successive flower resources throughout the growing season. The others – like *Eristalis arbustorum* or *Syritta pipiens* – treat this family as one of numerous potential pollen types that are eaten throughout the season. *Sphaerophoria stricta* in turn is interested in pollen from other families and from Apiaceae it picks up pollen of summer species and *Anthriscus sylvestris*.

The evidence that hoverflies have some preferences, can also be found in insects feeding on broader spectrum of flowers. Moreover, these preferences may alter throughout the growing season. Autumn faeces of *Sphaerophoria stricta* (n=6) contain almost exclusively *Polygonum aviculare*, *Spergula* and *Cruciferae* (2 or 3 types in different composition). A small admixture of *Anthemis* t., *Bidens* t. and *Arenaria* t. is noted only in one spectrum. *P. aviculare* pollen is not preferred by *Sphaerophoria* in summer. On the same area and period the guts of *Eristalis tenax* (n=6), *E. pertinax* (n=1) and *Helophilus trivittatus* (n=1) contain *Anthemis* t. (probably *Tripleurospermum inodorum* – a pollen type most frequently eaten by *Sphaerophoria* during summer and late spring), one or two types of *Cruciferae* and *C. Liguliflorae* and small admixture of *Fagopyrum* and *Polygonum persicaria*. Probably this pollen composition may result from decreasing flower resources in the late summer and an increase in the competition pressure. For this reason, in this time interval the faeces of small species of hoverflies contain pollen of small plants – *Polygonum aviculare*, *Spergula* or *Arenaria* – flowers of which are hardly available for larger syrphids. For the same reason, on *Eryngium planum* flowers – small syrphids can be often observed.

It is too early to estimate the scale of pollen consumption of particular species of Apiaceae, as well as dietary needs of hoverflies in respect to Apiaceae or to determine the pattern of selectivity of particular species of the examined hoverflies. According to the diagram this scale depends on the insect sex and size. Syrphids consuming Apiaceae pollen seem to be in some degree selective in their diet. Thus e.g. *Eristalis arbustorum* often eats pollen of *Carum*, *Libanotis*, *Chaerophyllum bulbosum* as well as *Daucus*, and *Myiatria sibiricum* pollen. According to the data obtained so far, pollen of some Apiaceae are eaten to a lesser extent by hoverflies – e.g. *To-*

rilis or *Angelica archangelica* (in case of the last taxon – despite its often visitations).

Apiaceae pollen in sediments

Members of Apiaceae family are commonly found both in towns in the areas with moderate anthropopressure level, as well as in the agricultural landscapes. Most of Apiaceae are rather light demanding species spreading on forest margins, meadows, pastures, dry grasslands and in ruderal habitats. Because of their life cycle only some of these species appear in croplands as weeds (e.g. *Aethusa*, *Caucalis*).

Pollen grains of Apiaceae found in sediments are well preserved. Signs of pseudogermination are rarely observed (Fig. 8: 26–29). Some pollen grains show lack of endexine (Fig. 8: 18–25, Fig. 7: 15–17) which suggests that they have passed through alimentary canals of birds or bats (Bińska 2003).

The list of Apiaceae found in the sediments is as follows (pollen types according to Punt 1984):

Laserpitium latifolium L.

Pollen grains of *L. latifolium* (Fig. 9: 9–13) are similar to *Laserpitium siler* (species with more southern range, absent from the Polish flora) and sometimes they are combined in one type (Mulder and Janssen 1998). Today rare localities of this interesting plant are situated in the two main areas – in upland and mountain areas in the southern and southeastern Poland and in the northern part of the country in the belt of high moraines – in the Mazurian and the Kaszuby Lakelands (Zajac, Zajac 2001). Such distribution suggests that the origin of some lowland sites could be relict in character. They are reported from pine-oak forest in Pomerania (Czubiński 1950) and from thermophilous communities of *Geranium sanguineum* or *Quercetalia pubescentis* in the Podlasie region (e.g. Ćwikliński *et al.* 1987).

Pollen of *L. latifolium* is present at Błędowo in the Younger Dryas (zone B2) and the early Preboreal sections (beginning of zone B3) (Fig. 9: 9–12). As it prefers soils rich in calcium carbonate (like *Pleurospermum austriacum*) it seems that this edaphic factor was responsible for expansion of this species in the Younger Dryas.

Pleurospermum austriacum (L.) Hoffm.

This species, due to its characteristic pollen features, was most frequently identified member of Apiaceae in the Pleistocene deposits. Now it occurs rarely in mountain areas in southern Poland, in sub-mountain zone and in relict lowland populations in the Kaszubian Lakeland and the lower Vistula River. According to Iversen (1954) the lowland sites of this species get scarcer westward into western Europe and its occurrence is limited by the -2°C isotherm of January. In lowland localities (Markowski and Chojnacki 1987, Herbich and Markowski 1998) it appears on young freshly slumping slopes, rich in calcium carbonate. This edaphic feature is of crucial importance in the distribution of *P. austriacum* balancing the influence of other unfavorable factors. It usually retreats from the vegetation in more mature succession stages. A good example of these relationships is the occur-

rence of *P. austriacum* in the Radunia valley, northern Poland (Herbich and Markowski 1998) where it grows together with other mountain species (*Bupleurum longifolium*, *Chaerophyllum hirsutum*, *Laserpitium latifolium* and *Libanotis pyrenaica*) in the *Stellario-Carpinetum typicum* community and it constantly migrates within this area. Similar observations were made on the slopes of the Vistula River valley (Herbich 1974) where *P. austriacum* grew in xerothermic vegetation.

In the late glacial sediments at Błędowo only a few pollen is found (Fig. 10: 27, 29). In the whole Pleistocene material analyzed in the present paper, most pollen was noted in the cold phases – at Świnna Poręba (22 pollen – Brörup, Fig. 10: 26, 30), at Kalińów (2 – open phase below the Holsteinian, the oldest finding, Fig. 10: 28), boreal phase at the end of the Eemian (3), at Zbójno (1) and rarely in the warm interglacial stages – at Zakrze (1 – *Carpinus* zone, Holsteinian), at Woskrzenice (1 – *Taxus* zone of the Holsteinian) and at Dziewule (1 – end of *Corylus* zone, the Eemian). SEM photographs (Fig. 10: 25–26, 30–31) and LM analysis of older material show no differences in comparison with the present day reference pollen. Other records of *Pleurospermum* in the Pleistocene were cited by Środoń (1970) and more recently by Noryskiewicz (1978) at Nakło (the Late Saalian), Krupiński (1995) at Ossówka (Holsteinian), Ralska-Jasiewiczowa and Demske (1998) at Gościąg (Late Vistulian) and Latałowa (1982) at Żarnowiec (Preboreal).

Berula erecta (Huds.) Coville

Only one pollen grain was found in the middle Holocene at Błędowo (Fig. 11: 22). Today *B. erecta* occurs in streams and rivers in the *Sparganio-Glycerion fluitantis* (Matuszkiewicz 1981). As the Błędowo Lake had no natural tributaries, pollen could reach the lake only when transferred by insect and/or birds. It is also not excluded that during the rarely occurring freshets, the waters of the nearby Wkra River were discharged into the lake (Bińska *et al.* 1991).

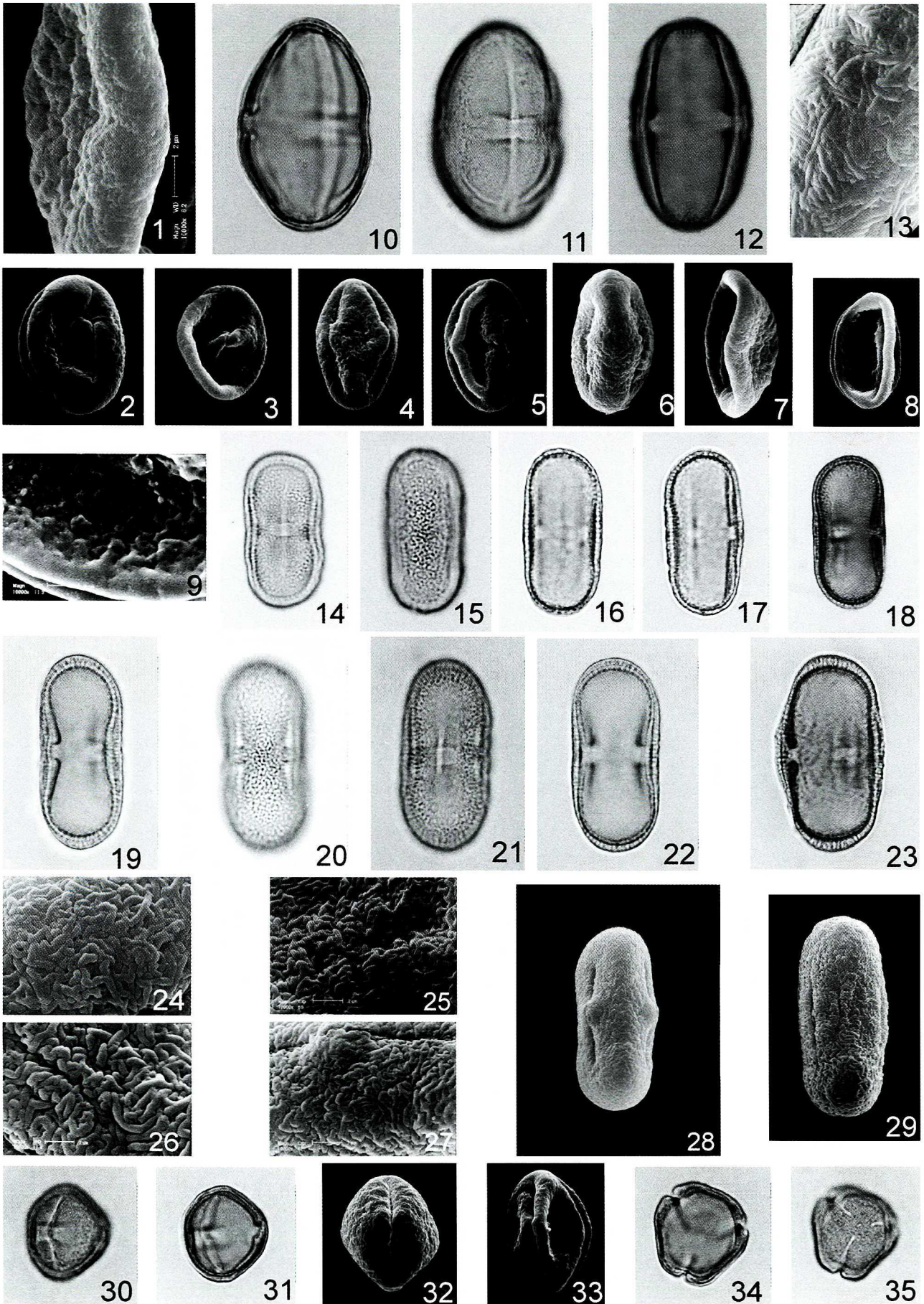
Pollen of *B. erecta* (Fig. 11: 18) is similar to that of *Sium latifolium* (Fig. 11: 17, 19) and differs only by smaller size.

Pastinaca sativa L.

This complex taxon (Loos 1993) is divided amongst other into *P. sativa* subsp. *sativa* (incl. cultivar var. *sativa* and var. *pratensis* Pers) and wild *P. sativa* subsp. *sylvestris* (Mill.) Rouy & Camus. In Poland only the wild taxon (var. *pratensis*) occurs commonly, showing increasing number of new sites similarly like in Germany (Loos 1993).

P. sativa is considered as an apophyte (Nowak 1983, Sudnik-Wójcikowska 1987), although it is hard to determine its original community. In the investigated area it more often grows in disturbed urban areas (roadsides, lawns, near rail tracks) than in rural ones. *P. sativa* is not evenly distributed across Poland and even in particular smaller areas. According to the distributional maps (Zajac, Zajac 2002), it occurs abundantly in southern and western regions of our country.

P. sativa pollen (Fig. 7: 18) differs from *Heracleum sphondylium* (Fig. 7: 19–22) by a smaller size and the character of collumelae. These taxa, together with *Malalabia* and *Tordylium*, represent a closely related pollen group.



At the Błędowo this easy to identification type (two specimens) was found only in the deposits younger than several hundred years (Fig. 12, Fig. 7: 14–17). However, macrofossils of *Pastinaca* were reported in older deposits e.g. from open (steppe-like) vegetation of Pleistocene (Mai 1992), since the Roman period in Germany (Körber-Grohne 1995) as well as from the Early Medieval in Poland (Latałowa 1999). A very late occurrence of *Pastinaca* at Błędowo as well as the absence of its pollen in the older Pleistocene units analysed by myself supports the view of Körber-Grohne (1995) and Loos (1993) that this species is a relatively new member in the Central European flora.

Daucus carota L.

D. carota is one of the most common Apiaceae in Poland inhabiting all kinds of disturbed areas and pastures of *Arrhenatheretalia* (Matuszkiewicz 1981, Nowak 1983).

The occurrence of pollen grains of *Daucus* started at Błędowo as early as the Allerød (Fig. 12, zone B1) and they were sporadically noted in the Younger Dryas (zone B2) (Fig. 10: 23–24) and in the first half of the Holocene. Since the *Carpinus* zone, carrot occurred abundantly in three phases – at the beginning of the hornbeam phase, just before and during the Roman period and from the Early Medieval till today. Since the Early Medieval somewhat different pollen (cultivated plants?) appears, however no special studies were undertaken. Pollen grains of carrot were also found in the Eemian at Nidzica (Bińka, Nitychoruk, in preparation).

Conium maculatum L.

Poison hemlock is a nitrophilous plant occupying open or semi-open, sufficiently moist habitats rich in organic matter (alliance Eu-Arction, Matuszkiewicz 1981). It may act as a pioneer species quickly colonizing wastelands. In the investigated area this species is rarely noted. It is an archeophyte originating from the so called, „Irano-Turan” region (Sudnik-Wójcikowska 1987). *Conium* pollen (Fig. 10: 19–22) was found in the youngest section in the profile from Błędowo.

Aethusa cynapium L.

A. cynapium rarely inhabits primary habitats (e.g. *A. c.* ssp. *cynapioides* (M. Bieb.) Simk (*Bidentetea tripartitae*, Rothmaler 1988) and it often grows in secondary ones (subsp. *agrestis* (Wallr.) Dostal, in gardens – in the alliance *Fumario-Euphorbion* (Rothmaler 1988) and in croplands – in the alliance *Caucalidion lappulae* (Matuszkiewicz 1981).

Only three pollen grains were found in the older parts of the Holocene (Fig. 9: 23–24). High requirements of *A.*

cynapium according to the content of calcium carbonate might be the possible explanation. Soils of the early Holocene were richer in calcium carbonate than now. Macrofossils of *Aethusa* were rarely found in Holocene sites – on Wolin Island (early Medieval, Latałowa 1999), in the vicinity of Krakow and Przemyśl (the late Holocene, Żmuda 1914, Kulczyński 1932, Koperowa 1970) and in other sites.

Anthriscus sylvestris type

This pollen type is represented by two very closely related species – *A. sylvestris* (L.) Hoffm. (one of the most common Apiaceae members in Poland) and *A. nitida* (Wahlenb.) Hazslinszky with pollen grains, which cannot be distinguished from each other, and for this reason they are combined in one type (Punt 1984). According to Doing (1962, after Spalik 1997) the first taxon originally is found in riverside forests of *Alno-Padion*. *A. sylvestris* occurs also in different types of vegetation (natural or anthropogenic) across Poland – *Arrhenatheretalia*, *Filipendulion*, *Arction* and many others occurring on partially shaded roadsides, rarely mown meadows and forest margins. The occurrence of the second species is restricted first of all to the southern part of Poland – mountain and sub-mountainous areas, where it occurs mainly in mountain deciduous forest (Spalik 1997).

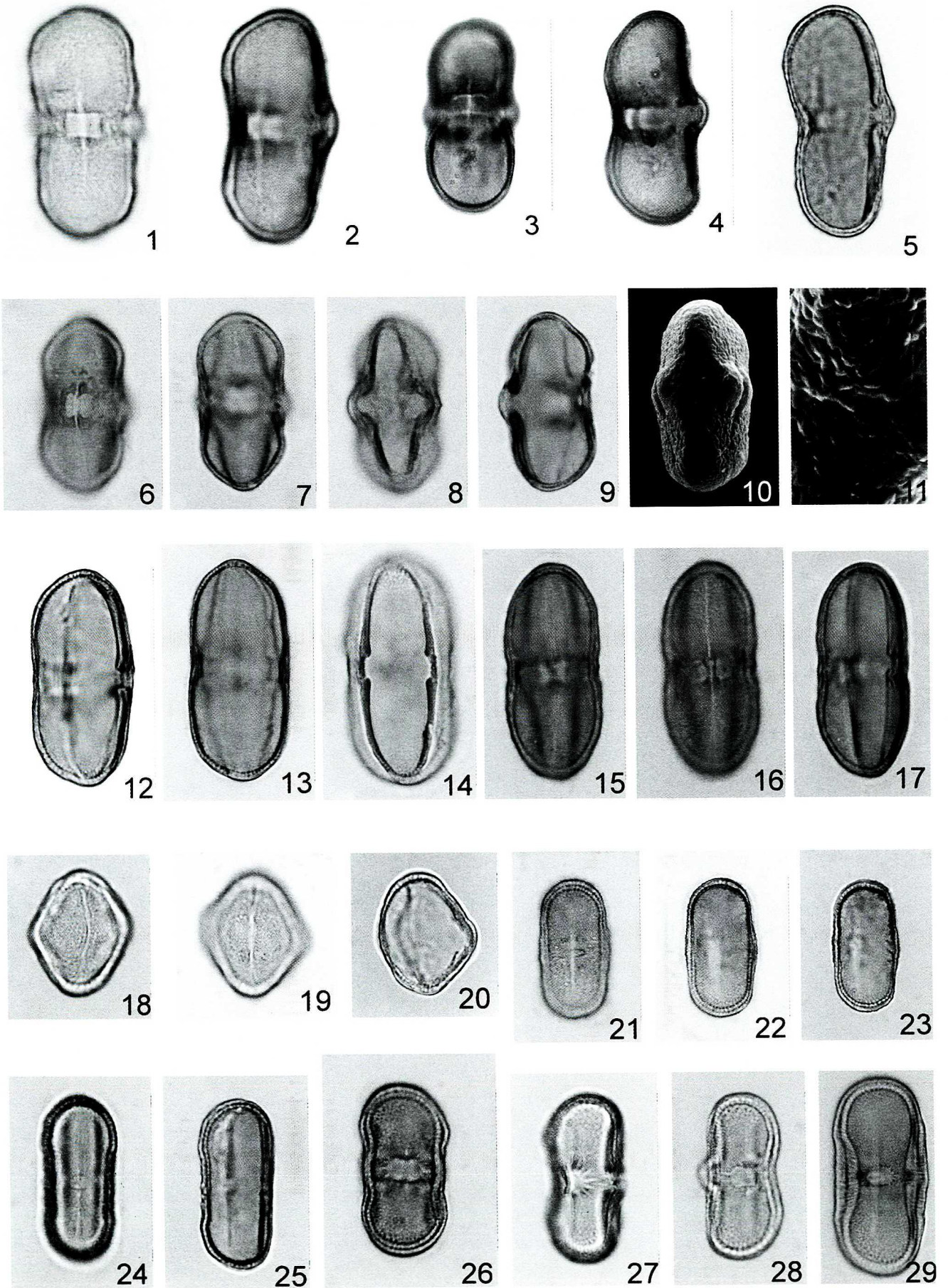
At Błędowo, pollen grains of *Anthriscus* appear very early in the Allerød (zone B1) (Fig. 10: 14–15), do not decline in the Younger Dryas (zone B2) (here *A. nitida* is probable) and rarely occur throughout the Holocene. The older findings of this type are from the Podlasie region (beginning of the Pinus-Betula zone of the Holsteinian) and the Eemian/Vistulian boundary).

Falcaria vulgaris Bernh.

Pollen of *Falcaria* is easy to recognize by its long columellae in the mesocolpium area. Both in reference slides and in the fossil samples, pollen (observed in side view) with straight (Fig. 10: 8–9) or distinctly curved (Fig. 10: 6–7) inner contour was found. The second type is illustrated by Punt (1984). Specimens with a straight contour are most common and they resemble pollen grains of *Anethum graveolens*, having however, coarse collumellae in the polar caps and different sculpture (Punt 1984) (Fig. 10: 10–13).

The early appearance of *Falcaria* at Błędowo and its occurrence in the early phases of the Holocene is very interesting. In Poland, its native range today is restricted mostly to north-western and western areas and to south-eastern ones with a clear gap between them (Zajac, Zajac 2001). In Europe, *Falcaria* represents the Pontian type of range. It prefers warm habitats, rich in calcium carbonate and for this rea-

Fig. 7. Photographs of pollen of Apiaceae. *Bupleurum*, fossil pollen, Błędowo (Bł.) sample 22, SEM photographs, clearly visible psilate sculpture near the colpi and on the polar area, the pattern of mesocolpium – some kind of rugulata-verrucata (1, 3, 5, 7), Bł. 19 (2), Bł. 21 (4, 6), Dziewule 9.55, the Late Saalian, Podlasie region (8, 9). *Hacquetia epipactis*, modern pollen, side view (10), colpus view (11), mesocolpium view (12, 13). *B. ranunculoides*, modern pollen, Tatra Mts (30–35). *Pastinaca sativa*, fossil pollen, Bł. 287 (14), Bł. 284, pollen with dissolved endexine (15–17), modern pollen, Jedlica, southern Mazovia region (18). *H. sphondylium* ssp. *sphondylium*, modern pollen, Kew, Thames riverside (26, 29) and *H. sphondylium* ssp. *sibiricum* (19–22, 27–28), modern pollen, Stok Ruski, Podlasie region (19–22), fossil grain, Błędowo 34 (23). Differences in sculpture pattern: modern pollen, Czachówek, Mazovia region (27–28), fossil grains, Świnna Poręba, Carpathians, Vistulian (24), Dziewule 7.35, Early Eemian (25).



sons it is sometimes dragged along the warm railway embankments with marl debris. The ideal habitats are riverbanks. Kępczyński (1965) suggests that the slopes of the incised valley of the Wkra River (flowing near Błędowo Lake) with calcareous glacial tills offered excellent habitats during the northwards migration of xerothermal plants. Perhaps during the Younger Dryas (zone B2) and in the early Holocene this species migrated into adjacent areas, which were highly calcareous at this time. The lack of *Falcaria* pollen in the diagram above the sample 156 at the middle Holocene (Fig. 12) may be explained by leaching of calcium from the soils during the Holocene rather than by deterioration of light conditions. Surprising is the lack of modern stands of *Falcaria* in the Wkra valley and the whole Mazurian Lakeland. Probably, it was gradually eliminated from plant communities. It is also possible that it never reached more northern areas during the Holocene expansion.

Pollen grains of *Falcaria* were found also in the early phases of the Eemian at Dziewule (Bińka, Nitychoruk, 2003; Fig. 10: 1–5).

Cicuta virosa L.

This is a characteristic pollen type (sharing features with *Apium*, *Oenanthe*, *Sium* and *Berula*) with long and very long colpi. Because of its morphological variation, identifications in light microscope can be reliable only when at least a few specimens are examined. Typical *C. virosa* pollen (Fig. 11: 20) closely resembles that of *Oenanthe aquatica* (Fig. 11: 21). The features distinguishing from the latter species – almost straight inner contour, subacute polar cups (Punt 1984) or somewhat different shape of porus – are not always clearly visible. Also on SEM photos (Fig. 11: 1–11, 29, 30) the differences of sculpture are only faintly expressed. *O. aquatica* has a rugulate pattern with smaller rugae and with a smaller tendency to form roof-like structures. However, SEM photographs of the *Oenanthe* – *Cicuta* complex from Błędowo and older parts of the Pleistocene as well as modern reference material (Fig. 11: 1–11, 29, 30) show that it is possible in most cases to distinguish between these two species on the basis of sculpture features. *Cicuta* pollen from Vistulian site in northern Podlasie (Fig. 11: 10), had smaller grains in comparison to the typical ones (29–33 µm versus about 36 µm in modern pollen). In samples from the Younger Dryas (zone B2), pollen of *C. virosa*, in comparison with that from Allerød or the Holocene, shows greater variation in size and outline – especially shortening of the long axis and broad range of pollen index or type of polar cups (obtuse or acute) (Fig. 11: 14–16). Such atypical grains are difficult to distinguish from *Sium* pollen (Fig. 11: 17, 19), which is characteristic by a more regular elliptic shape than *C. virosa* and *O. aquatica* group (sensu Punt 1984) and thick nexine. Variability of pollen

shape is also noted in modern pollen collected from *C. virosa* growing along lakeshores at Błędowo.

C. virosa is usually found in the tall sedge beds of alliance *Magnocaricion* Koch 1926 forming an association *Cicuto-Caricetum pseudocyperi* Boer et Siss (Matuszkiewicz 1981).

At Błędowo, macrofossils and pollen of *C. virosa* were frequent as early as in the Allerød (zone B1), Younger Dryas and Preboreal periods (zones B2–B3), rarely later on and again more commonly since the Early Medieval time marking lowering of the lake water level.

C. virosa belongs to the species, macrofossils of which are most often found in lake sediments. Primarily it is reported from the cold mostly boreal pollen floras – in the Holsteinian in Poland (Nita 1999) and Finland (Aalto *et al.* 1992), at many Pleistocene East European sites (Wieliczkiwicz 1982), in Mid-Pleistocene section in eastern Poland (Środoń 1954). It is often noted in the pine-birch phases or in the treeless pre-Eemian and in the Vistulian of Poland and adjacent areas (Granoszewski 1993, Dyakowska 1939, Velichkevich, Mamakowa 1999, Tobolski 1991, Tołpa 1961, Hahne *et al.* 1994) as well as from numerous Holocene sites.

Sanicula europea L.

Only three typical pollen grains were noted in the Holocene section in Błędowo (the first grain in its early stage – sample 45) (Fig. 8: 12–14). Today in the investigated area *S. europea* is rarely noted in deciduous forests. Two pollen grains were found also in the *Carpinus* pollen zone of the Eemian in the Podlasie region (Fig. 8: 15–17).

Carum carvi L.

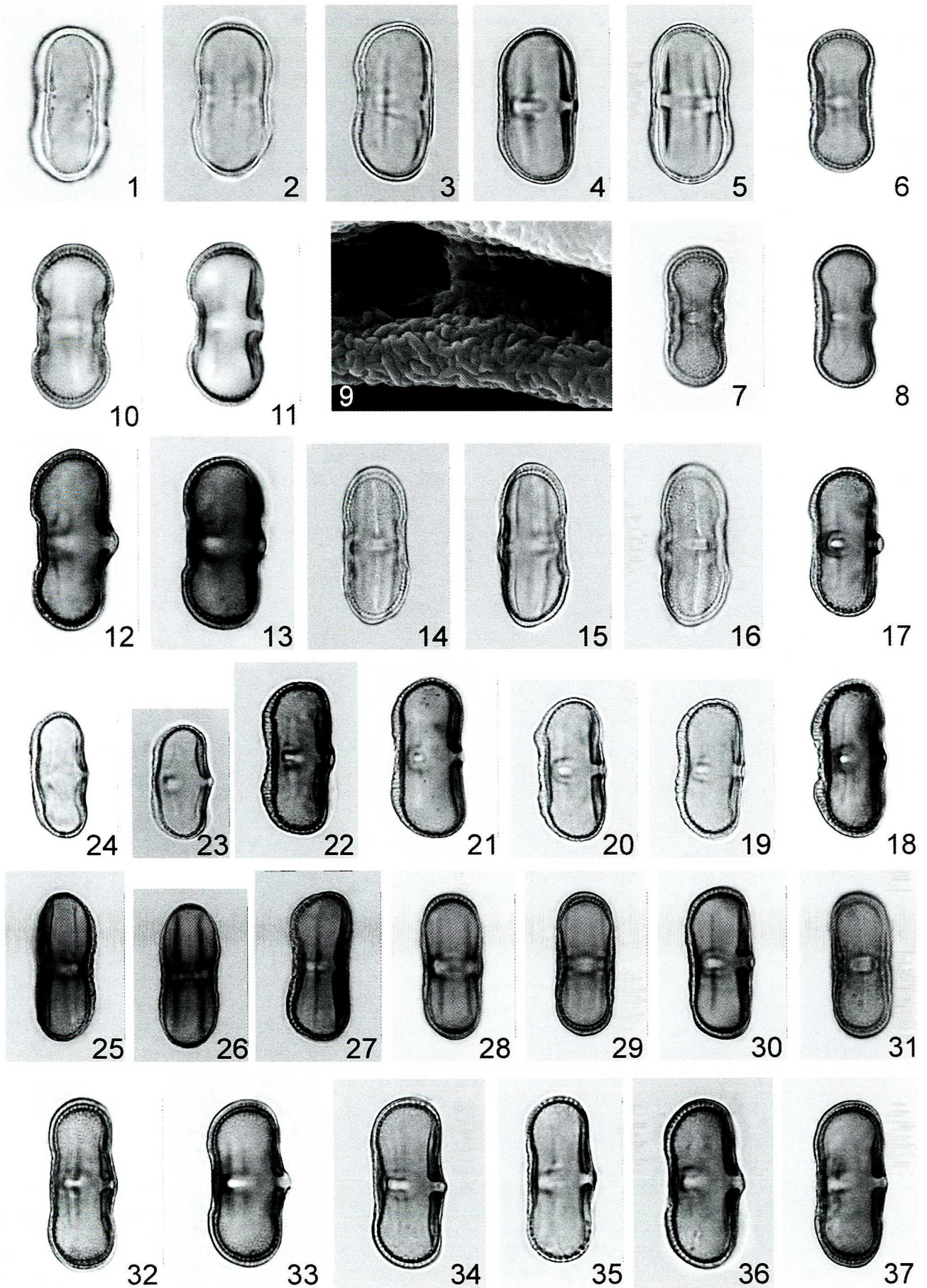
The pollen of this species is very rarely found in sediments at Błędowo (only four pollen grains noted in deposits) despite its quite common occurrence in modern communities. It appeared in the younger Holocene units but it has been completely absent since the Early Medieval. In this period, however, it should be expected in pollen spectra, taking into account its high light demands, which predestine it to grow in open landscapes created by strong human impact influence. Macrofossils (fruits) of *C. carvi* were found in the Dryas flora in the Carpathians (Kulczyński 1932).

Seseli annuum L.

According to Punt (1984) this species differs from *Libanotis pyrenaica* (L.) Bourgeau by its more elongated narrow endoaperture and indistinct columellae at poles (Fig. 10: 16–18).

Today both species are rare most often occurring on the slopes along river valleys (built by glacial tills rich in calcium

Fig. 8. Photographs of pollen of Apiaceae. 1–7 *Eryngium planum*, modern pollen, Góra Kalwaria, colpus view (1), side view (2), SEM photos, x2500 (10), x10000 (11); fossil pollen, Błędowo (Bł.) sample 22 (3, 4), Bł. 292 (5), Wilczyn (depth 3.75 m), the Holsteinian (6–9). 12–17 *Sanicula europea*, Bł. 45 (12–14); *Carpinus* zone, the Eemian, Podlasie region (15–17). Examples of pollen of Apiaceae with dissolved endexine, *Bupleurum*, Bł. (18–20), Apiaceae undiff., Bł. (21–25) and with pseudogermination evidence, Bł. Apiaceae undiff., (26–28), *Caucalis platycarpus*, Bł. 290 (29); 17, 18, 20, 27 – after Bińka, 2003.



carbonate), including valley of the Vistula River (Zając, Zając 2001). Therefore, Holocene occurrence of *S. annuum* at sites of the neighboring Wkra River was very probable. Kępczyński (1965) treats this species as a Pontic element in Polish flora. In the Błędowo section pollen grains are noted at the very beginning of the Holocene as well as in its middle part.

Torilis japonica (Houtt.) DC

Pollen of this species is characterized by typical bone shaped outline (Fig. 9: 6–8). At present this is the most common species growing in natural and anthropogenic habitats. Human activity undoubtedly increases the possibility of its expansion into new areas. *Torilis* is often found in ruderal habitats. The Late Holocene appearance of its pollen at Błędowo corresponds well to its numerous modern occurrences.

Chaerophyllum hirsutum L.

This plant in Poland grows mainly in mountain area and in two large lowland regions – in the northern part of the Mazurian and the Kaszubian Lakeland (Pawłow 1963). The lowland localities are situated on riverside meadows, along streams in wet and shady habitats or on wellhead areas.

Pawłow (1963) believed that these localities were formed during the postglacial expansion. This is probably true. In the Błędowo profile only four pollen grains were found in the Late Glacial and in the Holocene (Fig. 9: 35–36) so confirmation from other sites is needed. These pollen grains are similar to the modern (and subfossil) ones, which have somewhat different shape in various sites (e.g. these from Tatra Mts and Białowieża National Park have greater index than those from Kaszuby and Podhale (Fig. 9: 32–34, 37).

Eryngium planum L.

Six pollen grains were noted in the Błędowo profile: one in the Younger Dryas (zone B2), one in the Preboreal (zone B3) and four grains in sediments from historical period. The examined pollen resembles closely that of *E. planum* (Fig. 8: 1–2, 10–11) (a taxon absent in Punt's key) and it shares some features with Punt's *E. campestre* type. *Eryngium* forms a broad group of pollen with *Sanicula* (Fig. 8: 12–17) and *Hacquetia* (Fig. 7: 10–13). The length of fossil grains lies within the size range of modern pollen (32.5 – (36.4) – 41.6 μm , $n=50$). Fossil grains have short or rather long ectocolpus (differential feature of *E. maritimum* and *E. campestre*) widened above endoaperture, acute ends, margins rather vague, endocolpus short and broad – margins straight, ends diffuse, co-

stae broad, endocolpus somewhat apiculate with prominently raised sexine (Fig. 8: 3–5). *E. alpinum* has somewhat similar pollen, however occurrence of this species in Błędowo seems improbable. Today *E. planum* grows mainly in the Vistula and Bug River valleys and in anthropogenic habitats in adjacent areas. Difficult climatic conditions of the Younger Dryas (zone B2) probably allowed expansion of *Eryngium* along the rivers. Weiss and Ohana (1998) found evidence that in laboratory condition this plant flowered more intensively under moderate (22/17 °C and 17/12 °C day/night) than under higher temperatures (27/22°C or 32/27°C – only about 1% flowering plants). After the Younger Dryas expansion of *E. planum* into Vistula River and its tributaries, it probably retreated from some areas and persisted only on the slopes of the Vistula River valley. In historical times under more open conditions it again invaded this territory, where now it sporadically occurs in the vicinity of the lake.

This type of pollen was noted also in older deposits. In final stages of the Holsteinian one small pollen of *Eryngium* sp. (38 μm) with long ectoaperture – up to the poles (like in *E. campestre* and *E. maritimum*), and distinct raised sexine above endoaperture was found (Fig. 8: 6–9).

Aegopodium podagraria L.

At present this species occurs in different, mainly semi-shaded habitats – natural or anthropogenic ones. At Błędowo its pollen grains (Fig. 9: 1–5) occur rarely up to the *Carpinus* phase, when expansion of *Aegopodium* was stimulated by gradually opening forest floor (human impact). In the Early Medieval its abundance decreased again.

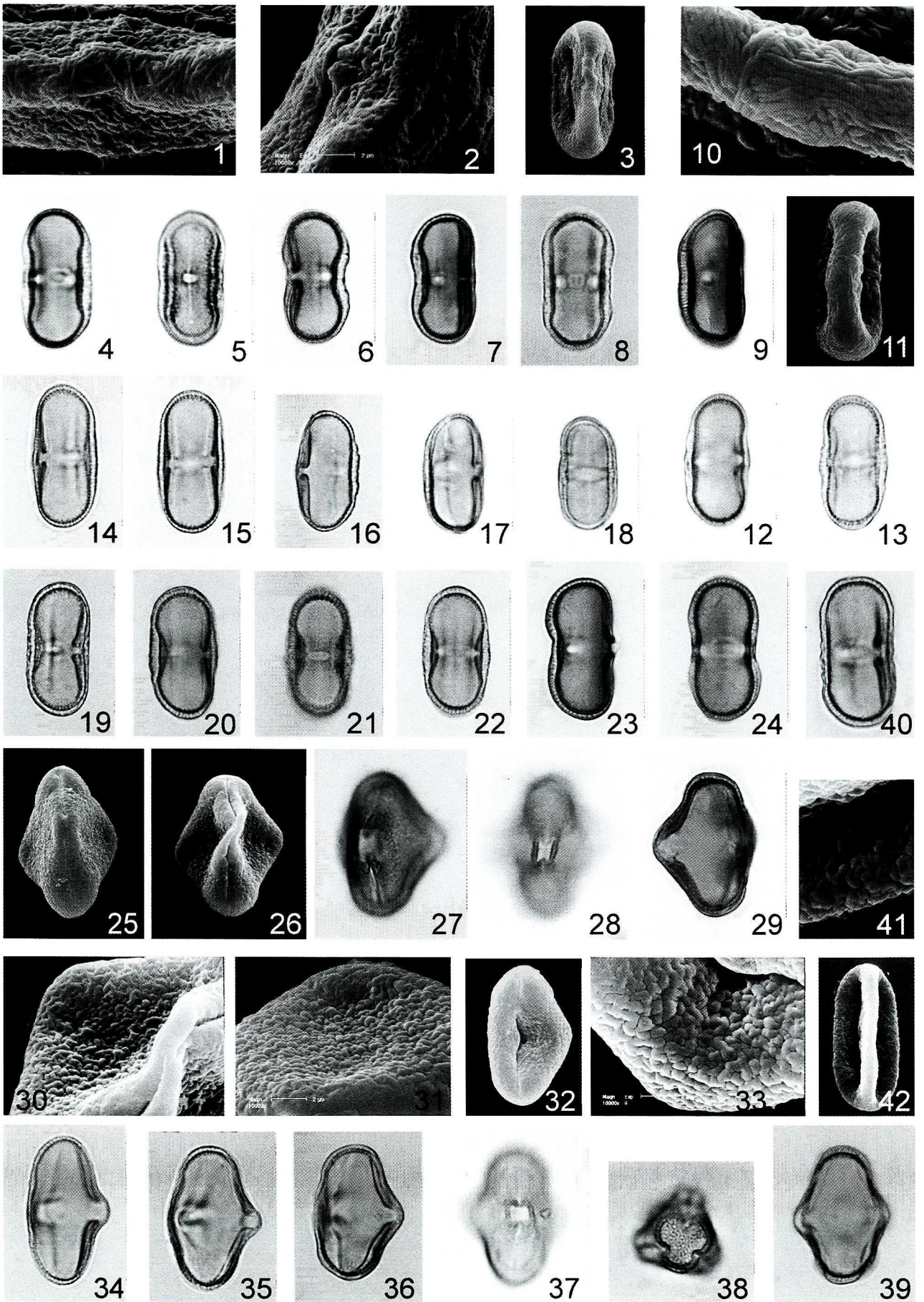
Ostericum palustre Besser

This is rather rare plant in Poland, occurring first of all at the Polish Lowlands and in the Lublin Upland (Zając, Zając 2001) in wet meadows on peaty soils. *Ostericum* pollen grains (Fig. 9: 14–16) are not abundant in the Błędowo section. Their maximum was attained in the initial stages of the Holocene but the earliest pollen has been found in the Younger Dryas (zone B2) (Allerød?).

Selinum carvifolia (L.) L.

This species grows in similar areas as the previous one, however it is more abundant in modern communities as well as in the pollen diagram from Błędowo. Its pollen in Błędowo (Fig. 9: 28–31) appeared at the end of initial zone of the Holocene and extinct in the middle of the *Carpinus* zone, probably due to the partial decline of wet peaty meadows close to the lake.

Fig. 9. Photographs of pollen of Apiaceae. *Aegopodium podagraria*, fossil grains, Bł. 210 (1–3), modern pollen (4–5). *Torilis japonica*, Bł. 36 (6–8). *Laserpitium latifolium*, modern pollen (13), fossil grains (9–12). *Ostericum palustre*, Bł. 64 (14–16). *Pimpinella saxifraga*, shape variation of modern pollen, Wojnów (17) and Stok Ruski, Podlasie region (18–19). *P. saxifraga* type, Bł. 61 (20), Bł. 19 (21), Bł. 21 (22). *Aethusa cynapium*, fossil grains Bł. 185 (24) and modern pollen, Łukęcin (23). *Angelica sylvestris*, Bł. 32 (25–26), Bł. 35 (27). *Selinum carvifolia*, Bł. 34 (28–31). *Chaerophyllum hirsutum*, modern material, Tatra Mts (32) and Kaszuby region (33), Białowieża National Park (coll. Eysymont, Drymer 1888) (34); fossil pollen, Bł. 21 (35), Bł. 32 (36) and from the travertine of Podhale region, the Holocene (37).



***Caucalis platycarpus* L.**

Rare modern localities of *C. platycarpus* are noted on calcareous soils in croplands in the upland areas (Zajac, Zajac 2001). Only one pollen grain was found in historical times in Błędowo (Fig. 8: 29), but this finding proved that this species in the past occupied a much broader range than nowadays. The species probably has been dragged in cereals transported along the Vistula River.

***Angelica archangelica* L. / *Angelica sylvestris* L.**

In the Punt's key these two species belong to two different types – *A. archangelica* type and *Peucedanum palustre* type but differentiating features in that key – the variation of columellae length between equator and shoulders – find no confirmation in the reference material of the author. Both equator and parts of shoulder show – especially in *A. archangelica* – a relatively large variability of collumellae length. The true difference is the inner contour, which is shallowly, continuously long curved in *A. sylvestris* and abruptly and shortly curved in *A. archangelica*. Differentiation of fossil pollen is difficult and uncertain. Features, which are common for these two types, include: coarse columellae at poles, irregular in cross-section and coarse tectum (LM).

In the Błędowo profile pollen of *A. sylvestris* (Fig. 9: 25–27) is noted relatively often and irregularly since the Younger Dryas (zone B2) and throughout the Holocene. Today it grows also near the Błędowo lakeshore. *A. archangelica* occurs sporadically in pollen diagram. If the last species is correctly identified it would mean that some of the lowland sites of this species may be native in origin, although it is treated as agrophyte in this area (Sudnik-Wójcikowska 1987).

***Pimpinella major* type**

This pollen type is often and willingly determined by palynologists. However, *Pimpinella* shows polymorphic features even within particular species forming the type – *P. saxifraga*, *P. major* and *P. nigra*.

In the Błędowo profile *Pimpinella* (Fig. 9: 17–22) is a common pollen type appearing very early (Allerød – zone B1). It is present in the Younger Dryas (zone B2) and common throughout the Holocene, declining slightly in its middle part. Most pollen probably represents *P. saxifraga* – a species at present commonly inhabiting open or slightly shaded dry places.

***Bupleurum falcatum* type**

Within Apiaceae *Bupleurum* represents a clear morphological type of pollen. The species occurring in Poland – *B. falcatum*, *B. tenuissimum* and *B. longifolium* are included in

the Punt's *B. falcatum* type. *B. ranunculoides* – a plant inhabiting the Tatra Mts, also represents this type. A special attention is drawn on the *B. longifolium* because this mountain plant has rare lowland sites (often with *Pleurospermum*) in northern Poland, where it migrated along Vistula River at the beginning of the Holocene (Czubiński 1950).

According to Punt (1984), *B. longifolium* is distinguished from other species by its larger size and convex-rhombic outline. However, in the fossil material from the Błędowo section as well as in numerous Pleistocene sections analyzed by the author, no grains with such features were noted. SEM photographs of modern and fossil material from Błędowo and older Pleistocene units show that all examined specimens exhibit the sculpture type similar to that of *B. falcatum* or *B. ranunculoides*, with hard to define shortly rugulate pattern visible only at mesocolpium (Fig. 7: 1–9, 30–35). Pollen with a clear and distinct microrugulate pattern at the mesocolpium and in the polar area, characteristic for *B. tenuissimum* (Punt 1984) is completely absent in the analyzed material.

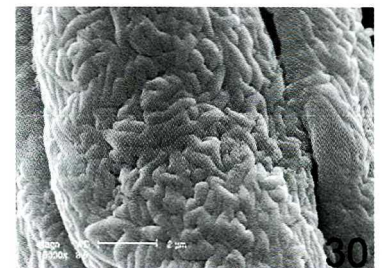
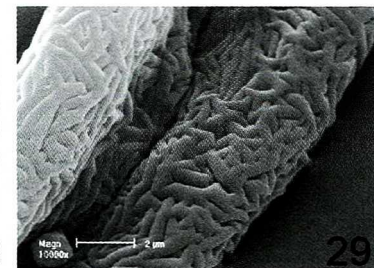
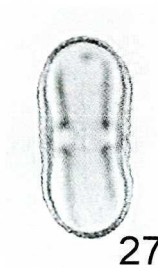
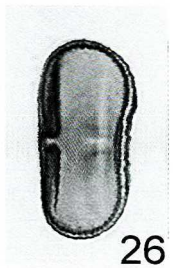
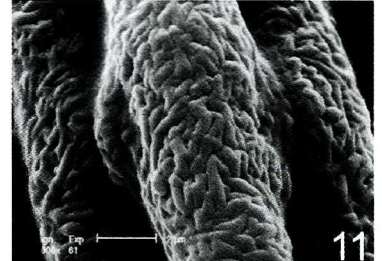
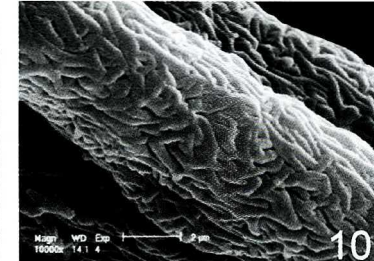
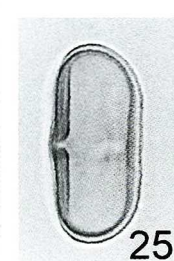
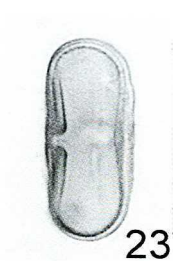
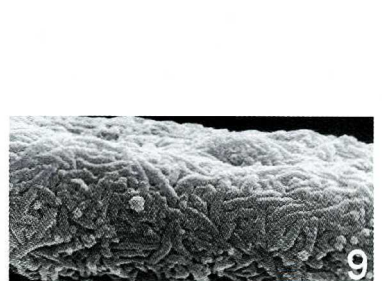
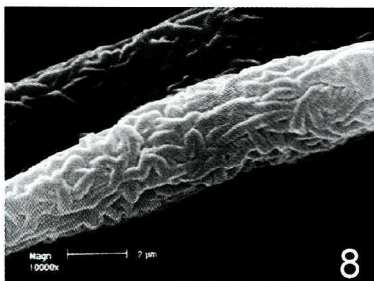
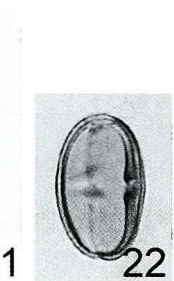
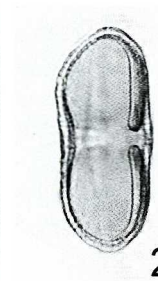
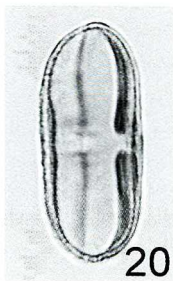
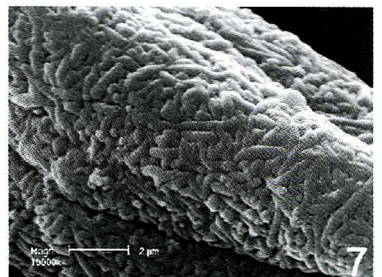
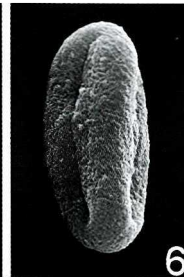
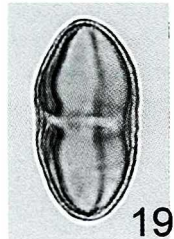
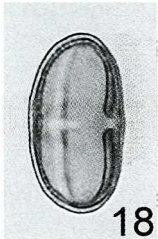
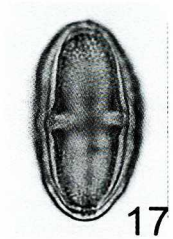
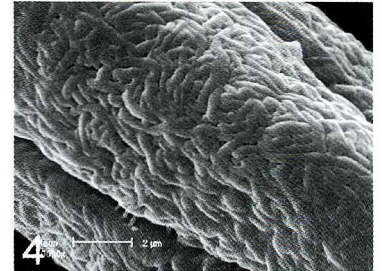
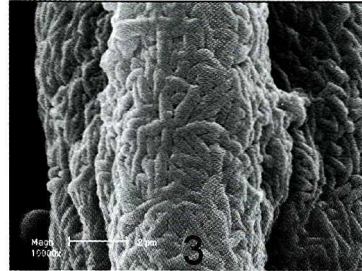
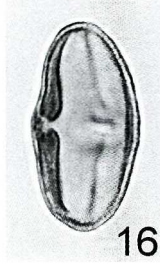
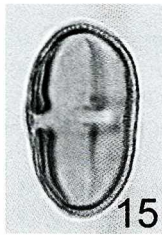
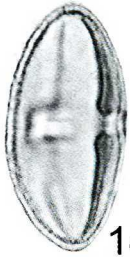
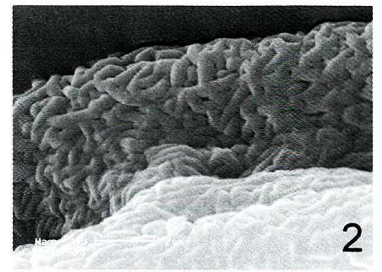
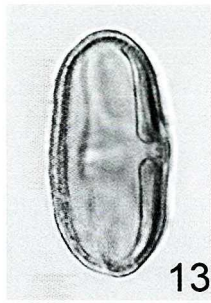
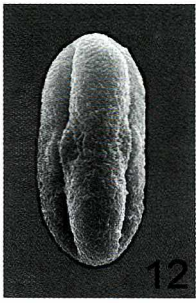
Bupleurum pollen is commonly identified type of Apiaceae in Pleistocene sediments that show open treeless phases before and after the interglacial. At Błędowo this pollen occurs mainly in the Late Glacial and only one grain was found in the *Carpinus* zone (*B. rotundifolium*?).

***Heracleum sphondylium* L.**

This species is represented in Poland in the lowland areas by two lower rank taxa – *H. sphondylium* L. subsp. *sphondylium* and *H. sphondylium* L. subsp. *sibiricum* – which, although forming one type, can be separated basing on morphology. The latter subspecies not considered in the Punt's *H. sphondylium* type (1984) has smaller grains (37.1 – (41.2) – 45.7 μm, n=50), generally smaller collumellae and the ectoaperture not ending in an area with indistinct columellae (Fig. 7: 19–22). The sculpture of *H. s.* subsp. *sphondylium* is formed by more prominent rugulate pattern (Fig. 7: 26, 29) than in the second subspecies (Fig. 7: 27–28). In half of the examined reference slides, collumellae at poles were significantly longer than in other areas.

In the vicinity of Błędowo *H. sphondylium* L. subsp. *sibiricum* occurs commonly (as well as in the north-eastern areas) while the second type is noted only sporadically. The precise range of both taxa in Poland is given by Gawłowska (1957). In Pleistocene sediments pollen representing *H. sphondylium* L. subsp. *sphondylium* is totally absent. All specimens analyzed are similar or identical to the second type (Fig. 7: 23–25). Specimens from the Holsteinian and the Eemian are smaller in size (about 36 μm – like in *Pastinaca*), however, with other features typical for *H. sphondylium* L.

Fig. 10. Photographs of pollen of Apiaceae. *Falcaria vulgaris*, differences in outline of modern pollen: specimens from Warsaw (6) versus this from Stara Warka (8), fossil grains: Bł. 18 (7), Bł. 17 (9), Dziewule 6.25, Quercus zone of the Eemian (1–5). For comparison with *Falcaria* type, fossil pollen of *Anethum graveolens* collected in the coffin from the hairs of dead person, Szeszto, historical times (10–13). *Anthriscus sylvestris* type, fossil pollen, Bł. 12 (14–15). *Seseli annuum* fossil pollen, Bł. 28 (16), Bł. 23 (17–18). *Conium maculatum*, fossil pollen, Bł. 294 (20–22), modern pollen, London, UK (19). *Daucus carota*, Bł. 26 (23–24). *Pleurospermum austriacum*, Bł. 19 (27, 29), Podlasie region, the early Vistulian (25, 31), Świnna Poręba (26, 30), Kalisz (28). *Ligusticum mutellina*, modern pollen, Tatra Mts (32–33, 36–39). Pollen of undifferentiated Apiaceae (Late Glacial of Błędowo) similar to *L. mutellina* type (34–35). *Ligusticum mutellinoides* modern pollen, Tatra Mts (40–42).



subsp. *sibiricum* (Fig. 7: 25). Pollen from the Brörup interstadial (Świnna Poreba, Fig. 7: 24, Bińka, Grzybowski 2001) in turn closely resembles in size the latter species.

Heracleum is noted most often in the initial pine-birch phases of interglacials and rarely in their final stages, infrequently in the temperate interglacial phases (*Carpinus* pollen zone in the Holsteinian, Eemian *Quercus* pollen zone) as well as in the boreal interstadials. Rare findings were noted in cold Pleistocene units.

At Błędowo *Heracleum* occurred since the Allerød, in the Younger Dryas (zone B2) and the initial postglacial pine-birch zone, rarely in later stages of the Holocene.

Peucedanum palustre (L.) Moench

Today this species often grows in the tall sedge communities near the lakeshores (like nowadays at Błędowo), and for this reason it is one of the most common pollen types in the examined section. In anthropogenic habitats it is noted on wet meadows or on embankments of ditches. Typical pollen of *P. palustre* (Fig. 11: 23–25) is recorded since the Preboreal (zone B3), particularly common in the second half of the Holocene.

Środoń (1974) noted macrofossils of *P. palustre* at the adjacent Góra Kalwaria in the Eemian. One pollen was identified in the final phase of this interglacial in the section from the Podlasie region (Bińka, Nitychoruk, in preparation).

Peucedanum oreoselinum (L.) Moench /*Peucedanum cervaria* (L.) Lapeyr.

According to Punt (1984) *P. oreoselinum* and *P. cervaria* pollen can be united in one type. Both species are not easy, nevertheless possible to distinguish. The main difference is the shape of endexine in the equator area – distinctly concave in *P. cervaria* and almost straight in *P. oreoselinum* (Fig. 11: 26–28). Since the very beginning of the Holocene, and especially in the later stages, the second species has been more common at Błędowo than the first one.

The late glacial and Holocene history of Apiaceae at the Błędowo site

The general curve of Apiaceae in the pollen diagram from Błędowo indicates that the majority of its occurrence is limited to the Late Glacial and the Preboreal (zones B1–B3) and the pollen zones B7–B9 (Fig. 12). In the opinion of some authors (Czubiński 1950, Kępczyński 1965) a key moment in the expansion of these light demanding plants is the Last Glacial and the very beginning of the Holocene. The Allerød (zone B1), incompletely recorded at Błędowo, begins with the expansion of *Cicuta* growing abundantly in shallow wa-

ter. *Anthriscus sylvestris* t., and *Pimpinella* occur regularly, along with *Falcaria*, *Heracleum* and *Daucus* (Fig. 12, 13). The list of 11 pollen types present in this period is obviously not complete, because a lot of pollen in the Allerød (zone B1) and in the Younger Dryas (zone B2) has not been identified.

The Younger Dryas did not terminate expansion of the Apiaceae (16 pollen types present) and for some taxa (*Bupleurum*, *Laserpitium latifolium*) that was the period of their highest frequency. Like other species of more southern modern range found in the Dryas floras (e.g. *Helianthemum*, *Gypsophila*), Apiaceae associated with the present day thermophilous grasslands of *Festuco-Brometea* – *Falcaria*, *Laserpitium*, *Eryngium*, *Seseli*, *Daucus* do not suffer from low temperatures and the short growing season. The existence of some species (e.g. *Falcaria vulgaris*, *Laserpitium latifolium*, *Pleurospermum austriacum*) in Allerød and in the following cold period would not be possible without sufficient supply of calcium carbonate, the source of which were glacial sediments of the Saalian, exposed after long erosional processes throughout the Vistulian.

The phase of pine–birch forest at the onset of the Holocene was the best period for Apiaceae development (17 pollen types present in the spectra) because of mild climatic conditions. *Falcaria* appearing as early as the Allerød (zone B1, Fig. 12), during the Preboreal (zone B3) found the best conditions for expansion on the fresh soils rich in calcium (Fig. 12). *Heracleum*, *Pimpinella* and *Angelica sylvestris* also occurred more abundantly at that time (Fig. 13). *Chaerophyllum hirsutum* began postglacial migrations from the mountains to establish its two large outlier populations in the Mazurian and in the Kaszuby Lakeland, as well as small single sites in the other parts of Poland. The new immigrants were also *Selinum* and *P. palustre* (Fig. 13).

In the successive pollen zones (B4, B5 and B6) a decrease of Apiaceae content took place (total pollen curve of this family, Fig. 12). The only taxa with higher frequencies observed in these zones are *Falcaria* and *Pimpinella*. Pollen of *Falcaria* dominates until the end of zone B6 and its decline corresponds with the decline of *Pteridium* (Bińka *et al.* 1991). Development of *Pteridium* is regarded as an indicator of fire (Oinonen 1967, Latałowa 1992, Ralska-Jasiewiczowa *et al.* 1998) and in the context of the Błędowo site it suggests the human factor as a cause. Fires probably stimulated erosion processes, which mobilized new calcium reserves, or caused an improvement of light conditions and made easier the persistence of *Falcaria*. Important for the expansion of *Falcaria* are very long roots with adventitious buds for vegetative reproduction. This adaptation enables to survive fires, cutting or destruction of over ground plant parts, as well as to persist long periods of unfavorable climate. Due to the presence of buds on the long roots *Falcaria* is believed to be a

Fig. 11. Photographs of pollen of Apiaceae. *Peucedanum palustre*, fossil pollen Bł. 273 (23–24), Bł. 19 (25). *Peucedanum oreoselinum*, fossil grains Bł. 251 (26), Bł. 30 (27–28). *Sium latifolium*, modern pollen, Łukęcin, Pomerania (17), Stok Ruski, Podlasie region (19). *Berula erecta*, modern pollen (18) and fossil grains, Bł. 190 (22). *Cicuta virosa*, fossil pollen, Bł. Late Glacial (12–16, 1), the end of Eemian and Vistulian, Podlasie region (from three sites) (10, 11, 29), modern pollen, Błędowo Lake (2, 20). *Oenanthe aquatica*, modern material, Lipnica (4, 5, 21) and from the Holocene, Podlasie region (9). *Oenanthe* sp., Podlasie region, Vistulian (3), Holsteinian (8) and Lower Pleistocene (6–7).

Błędowo

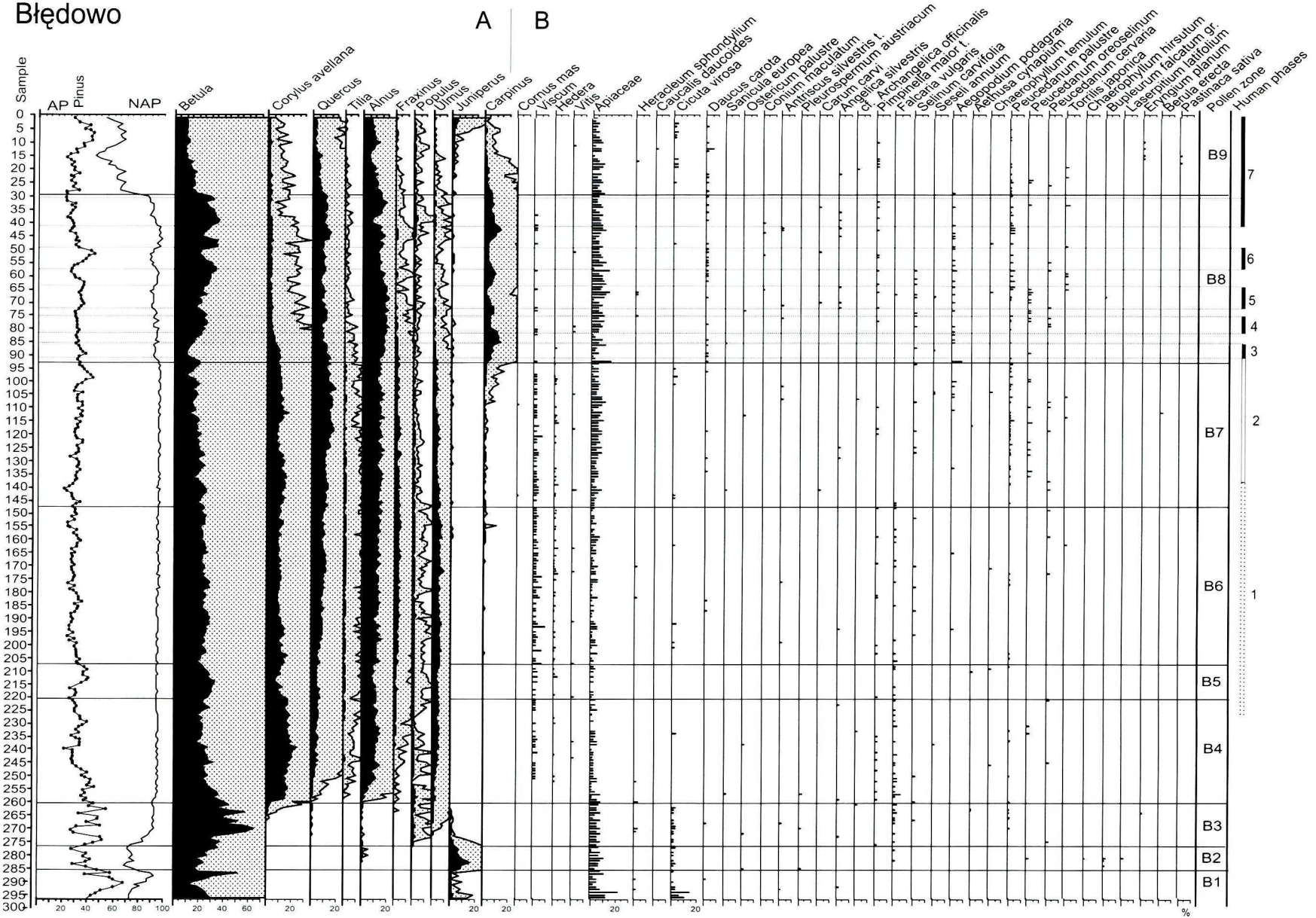


Fig. 12. Simplified pollen diagram from Błędowo. Part A – percentages of arboreal pollen and pollen zones after Bińka *et al.* (1991). Part B – histogram showing content of Apiaceae pollen in two pollen slides as well as pollen of some indicator taxa. Human phases: dotted bar – maximum content of *Pteridium* (fire evidence) in the Mesolithic and the early Neolithic (1), open bar – poorly defined human influence of the Neolithic (2). Black, filled bars – clearly defined younger human phases – Bronze – Roman (3–6), medieval – modern (7).

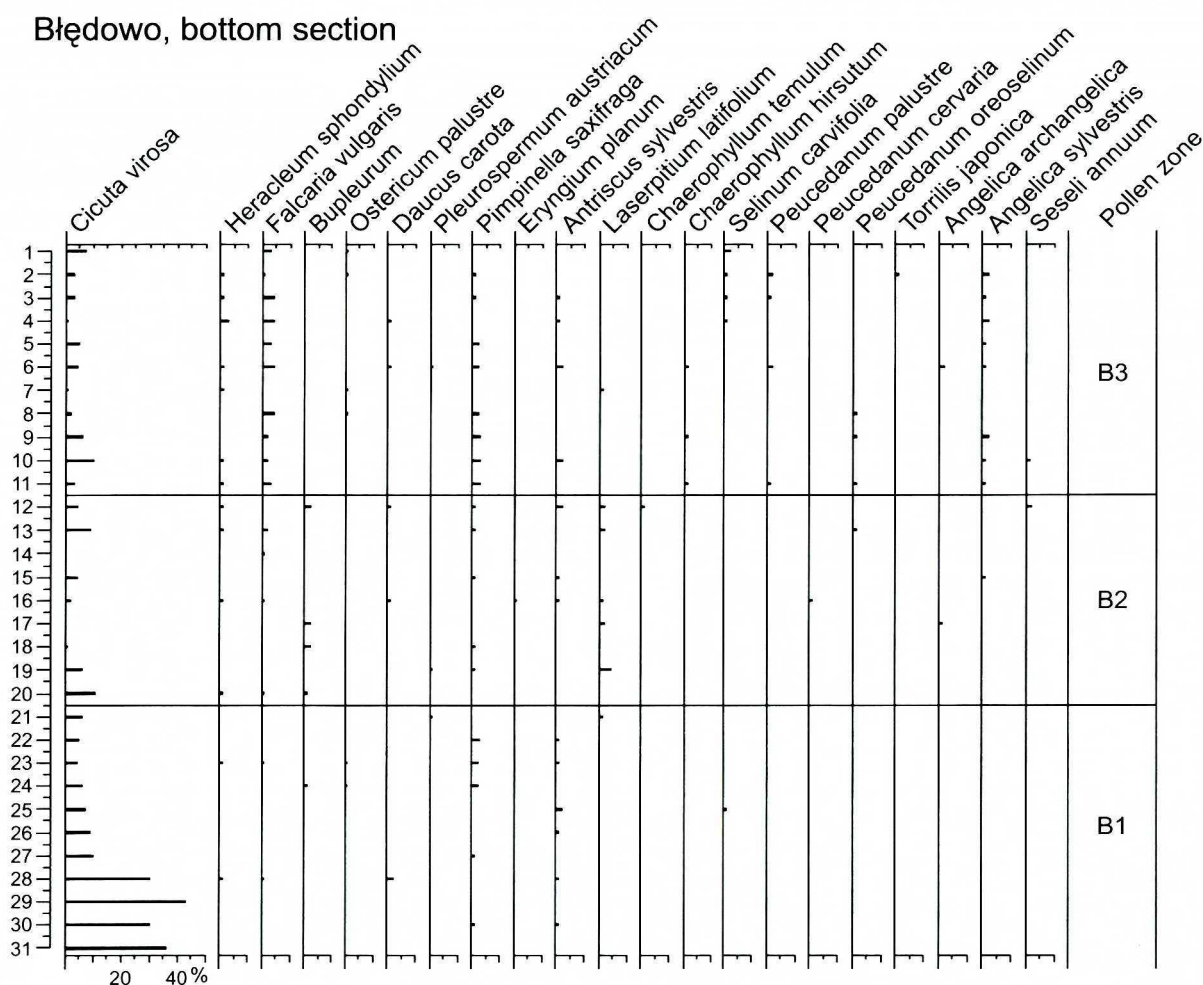


Fig. 13. Histogram showing the content of Apiaceae in the bottom part of section Błędowo III. Pollen zones after Bińska *et al.* (1991).

plant, which is hard to remove from natural communities and it is sometimes a troublesome weed in croplands. Additionally, with its long roots (over 1 m), *Falcaria* can penetrate deeper parts of soils, searching for calcium, an element successively eliminated from the upper horizons during the Holocene. The decline of calcium content in soils may be a potential reason, partly responsible for removing *Falcaria* from the communities at that time.

The zone B7 zone exhibits both a wide variety of pollen types and also higher values of Apiaceae in comparison with the previous zone, especially since the first appearance of *Plantago lanceolata*. More frequently four pollen types are noted: *Peucedanum palustre*, *P. oreoselinum*, *P. cervaria* as well as *Aegopodium* which occurred more abundantly at the end of the zone. The increased occurrence of Apiaceae is connected with basic changes in the forest communities, which find expression in higher, and more oscillating pollen curve of *Quercus* or rapid shifts of *Betula* in comparison with the previous zones. These changes could reflect coppicing or other forms of forest management (e.g. clearings), noted in many sites in the Neolithic (Latałowa 1992, Ralska-Jasiewiczowa *et al.* 1998). The possible effect was a creation of semi-shaded areas in the woods favorable for growths of Apiaceae but precluding development of open vegetation documented by rare occurrence of *P. lanceolata*. Gradually

opening forest floor can be observed in different forest communities – both in wet ones near the lakes inhabited by *P. palustris* and on the higher elevated dry places or on more fertile soils (*P. oreoselinum*, *P. saxifraga*, *P. cervaria*, *D. carota*, *A. podagraria*). In this group of plants only *Daucus* avoids forest communities and *P. saxifraga* tolerate forest habitats only under very good light conditions.

The ensuing zone (B8) with marked cyclic phases of settlement and forest regeneration is characterized by the maximum expansion of the Apiaceae family. In this zone, major rearrangement of forest cover took place. The high curve of birch with pronounced abrupt shifts, the cyclic incisions in the *Carpinus* curve, and the decline of pollen curves of some trees reflect the increased importance of clearings in forest management. In this zone increasing NAP frequencies suggest not only the higher proportion of open areas (such as pastures in the settlement phases) but also the establishment of croplands especially in the Roman period. *Daucus*, *Pimpinella*, *P. palustre*, *Angelica sylvestris* pollen types dominate in this pollen zone. Other pollen types – *Torilis*, *P. cervaria*, *P. oreoselinum*, *Selinum*, *Anthriscus sylvestris*, *Carum*, *Heracleum*, *Pimpinella* occur less abundantly, although more frequently than in the previous zones. Higher frequency of taxa representing almost exclusively open areas – *Daucus*, *P. saxifraga*, *Carum* or *Seseli* also attracts attention.

The zone B9 shows a still high content of Apiaceae pollen, however their successive decline can be observed (except of *Daucus*, *Cicuta virosa* and *Pimpinella*), probably due to the increasing anthropopressure. *Cicuta virosa* returned in higher frequencies into shore communities marking probably lowering of water table in the lake. The new floral element is *Pastinaca* (probably introduced into cultivation – var. *sativa* or var. *pratensis*) and *Caucalis* dragged onto the fields with seeds imported from southern Poland. Again, after the long absence, *Eryngium planum* returned, migrating along the Wkra River from the neighboring Vistula River valley.

A groups of Apiaceae which attract special attention because of possibility of the late glacial migration are: the mountain species (*Ligusticum mutellina* (L.) Crantz, *Meum athamanticum* Jacq., *Bupleurum falcatum* L., *Bupleurum ranunculoides* L.), mountain species with rare lowland sites (*Laserpitium latifolium*, *Chaerophyllum hirsutum*, *Bupleurum longifolium*, *Pleurospermum austriacum*, *Anthriscus nitida*), species with disjunctive arctic-alpine range (*Ligusticum mutellinoides* (Crantz) Vill.) or those showing mainly boreal range with sporadic sites in mountains of the Central Europe (*Conioselinum tataricum* Hoffm.). Concerning the first group a question arises if these species migrated to the lowland areas in the Late Glacial. Examining the *Bupleurum* type, it is often not easy to show the right taxon representing the Punt's *B. falcatum* group. The fresh postglacial soils, rich in calcium carbonate favored both *B. ranunculoides* as well as *B. rotundifolium* occurring nowadays mainly as field weeds in southern Poland. *B. falcatum* and some of the southern steppe species of *Bupleurum* can not be however excluded. The presence of *Ligusticum mutellina* on the lowlands in the Late Vistulian can also not be proved by pollen analysis. The occurrence in the late glacial section at Błędowo (zones B1-3) of a few grains resembling these of *L. mutellina* (Fig. 10: 34–35, 32–33, 36–39) requires confirmation by detailed analysis of sculpture on SEM photos. Grains of *Meum athamanticum* known from rare modern localities in the Sudety Mts. and scarce occurrences in the Suwałki Lakeland were also not found in the Błędowo samples. These pollen grains are morphologically similar to *P. austriacum* and for this reason they might not be always correctly identified.

The Pleistocene history of *Pleurospermum austriacum* forming the next group has been known for a long time (Środoń 1974). Most probably this plant migrated not only along river valleys, as believed previously, but it was present also out of them. Szafer (1930) described this species as a relict established in the lowland areas at the boundary of the Late Glacial and the Holocene. According to Czubiński (1950) it expanded into lowlands in the Preboreal pine-birch forests overtaking other migrating species – *Bupleurum longifolium*. It moved northwards along the Vistula River and its tributaries – the Bug and Narew River. Based on fossil data Środoń (1970) proved the common presence of *P. austriacum* in the Late Glacial in the non-mountains areas. It seems that Pleistocene findings of this species concern colder phases – rather before and at initial phases of interglacial (in pine – birch forests) than after them. This may be associated with the availability of suitable habitats, rich in calcium carbonate, due to

stronger erosion in the pre-interglacial environment. As mentioned previously, the lack of calcium carbonate in soil eliminates this plant from the vegetation. In Poland the late glacial history of *P. austriacum* started in the Older Dryas (Ralska-Jasiewiczowa 1966) and probably still earlier and its occurrence was not closely associated with the late glacial river pattern.

The other members of this group – *Laserpitium latifolium* and *Chaerophyllum hirsutum* – are present at Błędowo either in the Younger Dryas (zone B2 – the first taxon) or at the beginning of the Holocene (the second one). Probably at that time they migrated to their modern lowland sites. Maybe the late glacial findings of the *Anthriscus sylvestris* pollen actually represent its mountain relative – *A. nitida* showing similar pollen morphology. *Bupleurum longifolium* belonging to the same group and reported in modern lowland sites is also absent at that time at Błędowo as well as in many Pleistocene profiles in the treeless phases. The question is how, and when did this species migrate into the northern sites?

The present day geographical range of *Ligusticum mutellinoides* suggests that in the Late Glacial its disjunctive areas could have been united. Pollen grains of this species are poorly distinguishable and very hard to identify, so it might have been overlooked at Błędowo (Fig. 10: 40–42).

In the Late Glacial the reverse expansion, from lowlands into the mountains, was also possible. Rare mountain sites of *Conioselinum tataricum* showing north-eastern ranges also could have been inhabited in the Late Glacial. This pollen was not found at Błędowo.

DISCUSSION

The occurrence of Apiaceae pollen in sediments may be affected by five principal factors:

- a) richness of Apiaceae in plant communities;
- b) intensity of flower visitation and pollen consumption by insects in respect to their attractiveness;
- c) further dispersion of pollen to depositional basins by higher animals;
- d) richness and oscillations of animal populations;
- e) human influence.

It is obvious that frequency of selected taxa of Apiaceae is different in different habitats. In the study area some of them are rare species (e.g. *Ostericum palustre*, *Heracleum sibiricum* ssp. *sphondylium*, *Cnidium dubium*), the others (e.g. *Pastinaca*) are common in some sites but almost lacking in other sites. In effect, they may appear in variable proportion in the diagram.

Flower visitation rates by pollinators are different for different genera of Apiaceae and depend on the flower attractiveness (flower size and density, nectar quality) as well as on the presence or absence of local competitive plants of other families. For example, flowers of *Anthriscus sylvestris* and *Chaerophyllum temulum* are less attractive and more rarely visited than *Aegopodium podagraria* despite the similar pollinator composition and despite overlapping of blooming periods (Dlussky 1998). Similar discrimination concerns *Anthriscus sylvestris* and the very nectarous *Angelica archangelica* when inhabiting the same area. However, visitations may not correlate positively with the number of pollen

in the guts because, in case of *A. archangelica*, the insects consumed probably more nectar than pollen. Therefore the lists of plants considering their general attractiveness for insects (e.g. Ssymank 1991, Branquart, Hemptinne 2000) have a limited value for palynological/palaeobotanical conclusions and must be supplemented by the list of pollen consumers. However, the pattern described above may have a consequence in further pollen distribution and in pollen record. Pollen grains of *Chaerophyllum temulum* or *Anthriscus sylvestris* are rarely noted in pollen diagrams, despite the fact that these common species could have found suitable habitats throughout the Holocene. The high frequency of their modern occurrence does not correspond with its Holocene history illustrated by the pollen diagram.

Syrphids partition flower resources, and Apiaceae undoubtedly attract their attention, which has a consequence in the later transfer of pollen to sediments. Although different members of hoverfly communities visit particular species of Apiaceae with different frequency, it seems now that pollen grains of most of the Apiaceae species have rather similar chance to reach the guts of insects. The only exceptions are *Chaerophyllum temulum* and *Angelica archangelica*, the pollen of which was consumed less willingly (and plants of the first taxon visited more rarely).

The next issue is the prey selection by predators. Prey selectivity of bats or birds – taking into account the size of insect – often changes during the season, following the availability of insects. This selectivity undoubtedly influences the pollen transfer into lake basin. This issue requires further detailed investigations.

An important question, which can influence the frequency of pollen of some early blossoming taxa, is the relative absence of predators during their flowering. The time of blossoming and return of birds varies from year to year and it is hard to estimate their precise range. Both bats and insectivorous birds return quite late from their winter quarters, after the blossoming of the first Apiaceae and, which is more important, the time of feeding the progeny and consequently the significantly greater hunting activity take place still at later time. This might cause under representation of some Apiaceae pollen in sediments. Furthermore, the limited records of *Chaerophyllum temulum* pollen might be caused only by overlapping of its early time of blooming (similar as *Carum carvi* and *Anthriscus sylvestris*, both at the flowering stage earlier than *Chaerophyllum temulum*), with the arrival of insect consumers from their winter quarters e.g. barn swallows starting to build their nests. In case of *Aegopodium podagraria*, of similar flowering time as *Chaerophyllum temulum* this limited transfer is counterbalanced by the more frequent floral visitation by insects. Then again, late spring is the time when colder moments are often the case, inhibiting activity of pollen transfer agents. For these reason the late flowering (late summer-early autumn) Apiaceae (e.g. *Cnidium dubium*) could have a lesser possibility to reach the lake deposit, taking into account also climatic factors.

It is important to learn not only which animals are involved in pollen distribution but also to estimate the size of their foraging area and the fluctuation of their populations. Pollen brought in hoverfly faeces excreted on lakeshore plants or on drying littoral deposits, most probably comes

from plants growing around the lake. This range is hard to estimate and surely is different for particular syrphid species. Probably hoverflies move randomly when exploring their floral resources. This view is supported by observations of *Episyrhus balteatus* (Cowgill 1991, after MacLeod 1999) where only 1% of 2910 individuals marked with paint revisited the investigated area. Sometimes flight distances are large e.g. during yearly migrations more than 100 km per day (Ssymank 1991) or when pollen resources are limited (several km, Scheider 1958). The wide range of insect consumers – birds, bats, Asilidae and Odonata – would then accumulate pollen data from a large territory, however, their faeces would be deposited in a lake zone adjacent to the shore (several dozen meters wide), because this insect-rich belt is foraging area more useful for predators. It means that in deposits of the central part of lake, Apiaceae would be less abundant than near the shore. The influence of foraging area of predators is reflected in the fossil pollen spectra. The major differences in content of entomophilous pollen can be seen especially in the surface soil spectra collected from locations very close to each other, but representing different habitats in terms of foraging area of the predators. Another example are subsurface samples taken in arboretum in the center of the nearly closed stands and used as a nesting area of abundant avifauna, which reveal a rich spectrum of field weeds (e.g. *C. cyanus* and other) growing in a further distance.

A great role in pollen dispersion is played by *Hirundo rustica*, a common bird of agriculture landscapes. This immigrant species is characterized by high fluctuating population level (Møller 1989) in contrast to the resident species. The number of breeding pairs at a certain area varies significantly and may increase rapidly by even more than 100%. It is important from palynological point of view that the swallow population may be strongly influenced by some agricultural practices such as cattle farming. Studies of Møller (2001) showed that termination of dairy farming reduced the barn swallow population size by 48% on average, despite the fact that in all examined farms pastures for horses, sheep and other animals were still maintained around buildings. It is also worth noting that about 98% of barn swallow foraging (Møller 2001) took place within a distance of 500 m and 50% within less than 100 m from their nest site. It means that places lying outside these areas are very rarely visited, which significantly decreases the possibility of pollen transfer into depositional basin. Therefore the reduction of cattle farming or moving of farm buildings may change pollen influx into depositional basin.

Also in case of bats fluctuation in the colony size may result from anthropogenic factors. For example cutting down old trees with hollow scooped out trunk around the lake causes abrupt decrease of bats population and limits their flights above water surface and induces lack of some types of pollen in sediments. Situation of buildings near the lake supports some synanthropic species of bats. Warren and Witter (2002) showed that there is no significant change in the number of bats counted during the examined breeding season, while other investigators see large fluctuations in their number.

Fluctuation pattern of insect populations is much more complicated and each species of certain community can

show independent fluctuation. This is caused by complex and varied life styles, different larval habitats, type of range and many other factors, which may be affected by changes of climate (Owen, Gilbert 1989). According to Owen and Gilbert (1989) populations of hoverfly are more stable than other invertebrates. The prediction of the influence of such fluctuation on the possibility of pollen transfer is very difficult to estimate and needs to be related to the individual insect species. It is important that different communities of hoverflies inhabit various landscapes, e.g. mountains, forests, grasslands, moors or anthropogenic biocoenoses (Bańkowska 1980). Fortunately, bulk of most communities often form species common to almost all habitats with large geographical ranges (Bańkowska 1980). This pattern is blurred by strong anthropopressure (especially in urbicoenoses and agrocoenoses), which eliminates some syrphids from the environment, encouraging thus the most common ones. Hence it is simpler to trace the pollen influx because most grains are transferred by a relatively small number of syrphids species.

There is no doubt that the Apiaceae content and composition in pollen spectra in the second half of the Holocene was strongly affected by man. The first traces of human activity visible in pollen diagram from Błędowo (higher amount of *Pteridium* in the Mesolithic – early Neolithic zones B5-B6) are not accompanied by an increase of Apiaceae. However, in the Neolithic zone B7 where some openings in the forest cover caused by coppicing and clearings are noted, the successive increase in number of Apiaceae pollen grains is observed. Human impact is more conspicuous in the following zone B8 with clearly developed settlement and forest regeneration phases. However, it is difficult to match the increase of the pollen sum of Apiaceae and to correlate the appearance of the particular species with successive settlement events of the carrot family or pollen types with these distinct levels. Sometimes the decline and further restoration of some types e.g. *Daucus carota* coincide with boundaries of human influence periods (e.g. the end of the Roman period, beginning of the Early Medieval), however in other periods *Daucus* persisted longer or appeared earlier exceeding these boundaries. This refers to all pollen types of Apiaceae noted in the human impact phases, the concentrations of which started and ended at different moments and as a rule did not match the boundaries of the settlement phases. On the other hand *Aegopodium* is more often found in the regeneration zones of B8 than in the settlement phases, which is also an indication of human influence on this species.

The carrot family is rich in native taxa, which were commonly used in houses as therapeutic plants or spices. Amongst these plants, such herbs like *Sanicula europea*, *Eryngium planum*, *Anthriscus sylvestris*, *Conium maculatum*, *Cicuta virosa*, *Pimpinella*, *Oenanthe aquatica*, *A. archangelica*, some *Peucedanum* species or *Laserpitium latifolium* should be mentioned (Mowszowicz 1983, Paluch 1984). Picking of above-mentioned plants, probably had not influenced their population too much. However population of herbs, the green parts of which were used as vegetables, declined much more distinctly. In Poland such valuable vegetables were sprouts of *Aegopodium* (Mowszowicz 1983, Twarowska 1983) and *Angelica sylvestris*. Similar schemes would concern *Heracleum* (a short time ago a willingly eaten

plant, Twarowska 1983), occurring sparsely in the past Holocene periods despite its common presence in modern communities. Willingly consumed was also *Pastinaca sativa*, the pollen grains of which are noted only in historical times at Błędowo. It is hard to say whether this plant occurred in the older periods Holocene and then was drastically reduced by man or it was introduced into cultivation only at much later time. A similar herb is *Carum carvi*, very common and useful today, however only sporadically noted in the settlement phases of the zone B8. Other valuable herbs used as vegetable, *Anthriscus cereifolium* and *Libanotis pyrenaica* (Celka 1999) are absent in the Błędowo sediments. The latter plant grows today sparsely in Poland, but it was relatively often associated with medieval earthworks (Celka 1997, Buliński 1993), where it was frequently observed by the author (e.g. near the Early Medieval fortified settlement and castle at Czersk on the Vistula River, at Mielnik on the Bug River and on the castle hill at Olsztyn near Częstochowa, Fig. 1). The issue is if its restricted modern range is also an effect of consumption. Another species, *Falcaria vulgaris* occurred commonly in the Błędowo profile only in the first half of the Holocene. In some countries e.g. Armenia, sprouts of *Falcaria* are commonly picked by people in early spring – similarly as *Chaerophyllum bulbosum* (in Poland regarded as a relic plants connected with the Early Medieval settlements, Celka 1999) and then cooked with eggs and butter or consumed with sour milk and garlic. Perhaps, this is the true reason why *Falcaria* pollen disappeared above the zone B6 when Neolithic man collected edible wild plants quite intensively.

FINAL REMARKS

The appearance of Apiaceae in the pollen diagram from Błędowo is characterized by the fluctuation of their frequency observed on the macro scale level. Periods with better light conditions on the ground had a larger content of Apiaceae pollen in the spectra. This is especially visible in the Late Glacial and at the onset of the Holocene and in the period when human interference distinctly altered the landscape. It is also the case in older stratigraphic units where this family occurred abundantly in pine-birch boreal forests with somewhat open floor.

The main issue is to assess to what degree oscillations of Apiaceae curves in the pollen diagram reflect actual changes in vegetation. It seems that insect feeding preferences influence transfer of Apiaceae pollen to a lesser extent. Only some species of Apiaceae are less frequently visited by syrphids. The pollen frequency in the sediment profile seems to be more affected by the season of flowering, i.e. some Apiaceae flowering in the early spring under worse weather conditions are underrepresented in pollen spectra because of lower insect activity. Also very important is the small number of predators in this early season, which restricts the pollen transport. Fluctuations of predator populations, oscillations of food demands in the breeding season or size of foraging areas of the predators, can also influence pollen influx to the sediments.

In the case of entomophilous plant species, focusing of pollen influx around the lake as a result of specific patterns of

plant-animal interaction may deform the palynological picture of real vegetation composition. In other words, the same vegetation pattern at two sites may not be identically reflected in the course of pollen curves. This complex pattern to a large extent might be also vulnerable to random disturbance. The resulting effect can be random beginning or termination of Apiaceae occurrence in the pollen diagram, not corresponding with the clearly defined anthropogenic phases, despite the fact that a large part of umbellifers may serve as indicator for meadows, ruderal places and partly open forests.

The last issue is whether the type of basin affects the content of pollen of entomophilous plants. Shallow and small basins rich in emerged vegetation and broad belts of rushes may be more frequently visited by insects and their predators that induces higher faeces in the deposits. Similar effect can occur where animal impact is greater because of limited water availability in the vicinity.

The comparison of conclusions arising from analysis of entomophilous pollen found in different lakes at the same period or comparisons made between lake and terrestrial peat deposits, may lead to erroneous results because of different patterns of the transfer agents. To overcome all these problems it is necessary to recognize more precisely the directions, in which pollen of insect pollinated plants reaches depositional basins. This requires intensive collaboration of palynologists and entomologists and is particularly important in these days when a large part of traditionally cultivated areas declines and the opportunity to trace the insect routes may be missed. Moreover, a short time ago such common agents as swallows became much rarer because of closing down of dairy farms.

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