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Bees of xerothermic swards in the lower Vistula valley: diversity and zoogeographic analyses (Hymenoptera: Apoidea: Apiformes)

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ABSTRACT. In xerothermic swards and thickets at 17 research sites in the lower Vistula valley (N Poland), 253 species of bees (Apiformes) were recorded. Southern and southeastern species (Ponto-Mediterranean, Pontic and Mediterranean) accounted for 20% of all recorded species. Substantial differences in species composition, diversity, and dominance structure were found between research sites and also between small plots (about 3 ha each) within one reserve. A discussion of the origin of the fauna of the study area suggests that the migratory route along the Vistula river from the Podolye refuge (W Ukraine) probably played a major role, beside two other routes: along the Toruń-Eberswalde Proglacial Valley from Germany and across the Moravian Gate from the south. A northward decrease in diversity of southern and southeastern species was confirmed.

KEY WORDS: Hymenoptera, Apoidea, Apiformes, N Poland, lower Vistula valley, Pomerania, xerothermic swards, diversity, dominance structure, zoogeographic analyses.

INTRODUCTION

The valley of the lower Vistula has a rich flora of southeastern and southern origin. These are mainly aggregations of xerothermophilous plants, with numerous Pontic and Mediterranean species. Many botanists agree that the vegetation of this area is outstandingly azonal (CZUBIŃSKI 1950, SULMA 1959, SZAFER 1959), which aroused the interest of naturalists already in the early 20th century. Its vegetation was thoroughly studied by PREUSS (1912), who made remarkable contributions to our knowledge of Pomerania. Reserves of xerothermophilous vegetation of this region were described in detail by SULMA and WALAS (1963). Shortly afterwards, the plant cover of the area was investigated in detail by CEYNOWA (1968). The dry and warm slopes of the Vistula valley are covered by various communities of herbaceous plants, which in German are termed 'Steppenheide' and in Polish are also sometimes called 'steppe communities'. However, the word 'steppe' is ambiguous, so many researchers – both botanists and zoologists – prefer to use the term 'xerothermic swards (sites)' (e.g. SZYMCZAKOWSKI 1960, 1965) or 'communities of xerothermic vegetation' (SULMA, WALAS 1963, CEYNOWA 1968) or 'xerothermic sites' (LIANA 1973). As reported by Z. CZUBIŃSKI (1950), xerothermic plants are usually classified as Pontic or steppe elements, but some are Mediterranean or continental. The word 'xerothermic' is used to denote the plant and animal species that are more or less closely associated with warm and dry habitats. Thus its meaning largely overlaps with the attributive meaning of 'steppe'. Without going into details of temperature and humidity ranges preferred by xerothermic species, we decided here – as recommended by KUNTZE (1931) and others – to assign to this group only those species, whose centres of distribution are located in relatively dry and warm areas so that as the conditions change with increasing distance from their distribution centres, they tend to occur only in dry and warm sites, such as banks of valleys and sandy slopes with favourable exposure (KUNTZE 1931).

The rich vegetation is accompanied by a varied fauna, with a large proportion of southern species, described by SZYMCZAKOWSKI (1965), LIANA (1973), BUSZKO (1990), STACHOWIAK (1997), etc. The areas along the lower Vistula were penetrated by the first apidologists already in the early 20th century, but they reported on only single species (ALBIEN 1905, ALFKEN 1909, 1912). In the 1970s, detailed research on diversity of Apiformes in the studied steppe reserves was conducted by BANASZAK (1975, 1980). Later on, bee densities were assessed in the reserve 'Zbocza Płutowskie' by BANASZAK and CIERZNIAK (1994). Their results were supplemented with data reported by PAWLIKOWSKI and KOWALEWSKA (1998) as well as PAWLIKOWSKI and HIRSH (2002).

In 1998–2002, our research team initiated large-scale investigations into the diversity of Apiformes along the whole lower section of the Vistula: from the reserve 'Kulin' (near Włocławek) to the reserve 'Biała Góra' (near Sztum). Our investigations involved exclusively the xerothermic communities of herbaceous plants and shrubs on slopes of the river valley, most of them protected within nature reserves.

Our project aimed: (a) to continue the inventory and to evaluate the current state of the bee fauna in xerothermic communities in steppe reserves in the lower Vistula valley, on both sides of the river; (b) to assess the faunistic distinctness of the studied sites with respect to local environmental conditions; (c) to trace the migratory routes of bees in the lower Vistula valley and to evaluate the northward decrease in diversity of xerothermic bee fauna on the basis of current and earlier research.

GEOMORPHOLOGICAL CHARACTERISTICS AND PLANT COVER OF THE STUDY AREA

The lower Vistula valley is of varied origin. The southern part is approximately latitudinally oriented, formed by the wide (up to 20 km) Toruń-Eberswalde Proglacial Valley, created during the Weichselian glaciation, when the ice sheet covered the region of Pomerania. Near Bydgoszcz-Fordon the narrower water-gap starts, which is a deep valley crossing northwards the plateau of the lakeland. The water-gap section of the Vistula valley is much younger, as it has been shaped after the last glaciation. The valley is 5−10 km wide in this section. Banks of the valley are often over 60 m high and run down at an angle of 30–45º to the flood plain. In many places, slopes of the valley are cut across by erosional ravines, dissecting the neighbouring plateau over up to several hundred metres (KONDRACKI 1967).

The climate of the study area is characterized by a low humidity and the lowest precipitation in Poland. Long-term means of annual precipitation are 500 mm in Włocławek, 450 mm in Toruń, and 467 mm in Chełmno. The summer period accounts for 65% of annual precipitation. Annual mean temperature for this region is 7.9ºC and monthly means are −3.5ºC in January and 18.5ºC in July. The growing period lasts 210 days (KONDRACKI 1967).

The geological substrates are various types of clay and silt, or sometimes clayey sands. The soils are usually characterized by the presence of calcium carbonate, whose concentration ranges from about 10% in the upper horizons to 25% at the depth of about 50 cm (CEYNOWA 1968). The type of plant cover developed there depends to a large extent on degree of slope and calcium carbonate content. Insolation during the growing period is very intensive, reaching 8–9 hours a day. However, light conditions on the slopes are specific, depending on the direction and degree of slope.

The land relief, distinguished by many slopes with southern, southwestern and southeastern exposures, combined with low precipitation and soils rich in calcium carbonate, resulted in development of xerothermic plant communities, with many steppe species (CEYNOWA 1968). The first steppe plants appeared there probably together with the glacial tundra at the early stage of Holocene, characterized by a dry climate and lack of forest cover. The Vistula valley created favourable conditions for plant migrations. The species representing the cold *Stipa* steppes probably migrated from the east along the rivers Narew and Vistula. From the west, xerothermic species, including Mediterranean ones, dispersed along the Toruń-Eberswalde Proglacial Valley (SULMA, WALAS 1963). However, gradually the conditions were becoming less favourable for development of steppe vegetation because of competition with forest communities. Xerothermic vegetation survived only on steep slopes, whose colonization by forest was inhibited thanks to erosion. Only the initiation of human activity – sheep herding, firing and clearing of forests – enabled again the spread of xerothermic communities (CEYNOWA-GIEŁDON, WALDON 2001). Currently the lower Vistula valley is distinguished by unusually rich xerothermic vegetation, as compared with other areas of northern and central Poland (CEYNOWA 1968).

On the slopes of the Vistula valley, xerothermophilous plants form various herb and shrub communities and also invade some forest communities. CEYNOWA (1968) distinguished three main types of xerothermic sward: *Potentillo-Stipetum*, *Adonido-Brachypodietum* and the moderately xerothermic *Festuco-Silenetum*. The first association is very similar to Eurasian steppes dominated by *Stipa* species (feather-grasses). Its characteristic species include *Stipa capillata* and *S. joannis*. The association *Adonido-Brachypodietum* is closely related to the so-called meadow-steppes, known from areas located east of Polish borders. Its characteristic species include *Adonis vernalis, Brachypodium pinnatum, Campanula sibirica, Scorzonera purpurea.* The association *Festuco-Silenetum* is intermediate between *Potentillo-Stipetum* and the plant associations of sandy grasslands and is found in sites poor in calcium carbonate. Xerothermic thickets are represented in the lower Vistula valley by the association *Peucedano-Coryletum*, composed of some trees (*Quercus robur*, *Pinus sylvestris*, *Ulmus campestris*), shrubs (*Berberis vulgaris*, *Corylus avellana, Crataegus monogyna, Prunus spinosa, Rhamnus catarctica, Rosa canina*), and numerous herbaceous species, both xerothermophilous and mesohygrophilous. Such thickets often occupy edges of xerothermic slopes or shallow ravines and depressions of slopes. Herbaceous plants are often gradually replaced by shrubs. Particularly common are thickets dominated by *Prunus spinosa*. This shrub species as well as those mentioned above are attractive bee forage plants.

Typical patches of xerothermophilous vegetation usually develop on southern slopes with angles of 20–50º. The degree of cover by plants as well as the species composition of plant communities significantly affect the microclimate. CEYNOWA (1968) compared the diel variation in relative humidity and air temperature in three different plant associations on slopes of the Vistula valley near Płutowo near Chełmno. She found differences in soil temperature between the main two associations. *Adonido-Brachypodietum* proved to be exposed to much smaller fluctuations of soil temperature than *Potentillo-Stipetum*. Extreme soil temperatures often differed between those associations by more than 10ºC. Much smaller differences in soil temperature were observed between *Adonido-Brachypodietum* and the thickets dominated by *Prunus spinosa*. Thus the pattern of soil temperature variation depends to a large extent not only on external conditions but also on the specific type of vegetation. The dense vegetation of *Adonido-Brachypodietum* protects the soil from direct sunlight more effectively than the vegetation of *Potentillo-Stipetum.* The effect of multilayered vegetation in shrub communities on soil temperature is even more conspicuous than the influence of *Adonido-Brachypodietum*. It is more difficult to interpret differences in air temperature and humidity between the associations. The differences are variable, dependent on air movements to a large extent. The highest values of air temperature were recorded in *Potentillo-Stipetum*, while the highest humidity in *Adonido-Brachypodietum*.

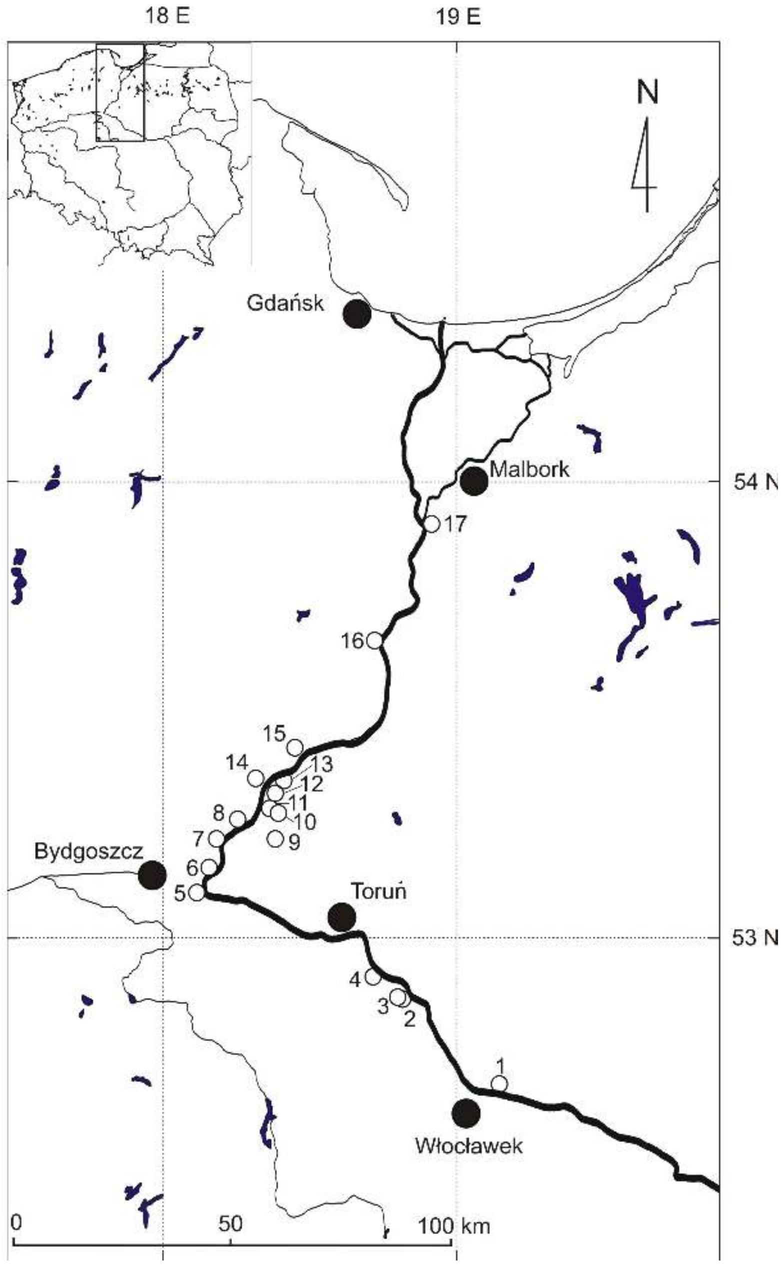

Fig. 1. Lower Vistula valley: distribution of research sites: 1 = 'Kulin'; 2 = Raciążek; 3 = Ciechocinek; 4 = Otłoczyn; 5 = Łęgnowo; 6 = Bydgoszcz-Fordon; 7 = Strzelce Dolne; 8 = 'Kozielec'; 9 = Unisław; 10 = 'Zbocza Płutowskie'; 11 = Kiełp; 12 = Starogród; 13 = 'Góra Św. Wawrzyńca'; 14 = 'Gruczno'; 15 = Świecie; 16 = Nowe; 17 = 'Biała Góra'.

STUDY SITES

Bees were studied at 17 xerothermic sites in the lower Vistula valley (Fig. 1), which are briefly characterized below.

1. Reserve 'Kulin' (UTM GD73). The study site is located on very steep and high (up to 90 m) slopes of the Vistula valley near Włocławek. Patches of xerothermic sward are scattered, separated by shrub communities. The eastern part of the reserve is the only lowland locality of *Dictamnus albus* in Poland. Two steppe associations have been distinguished in the reserve: *Potentillo-Stipetum* and *Adonido-Brachypodietum*, as well as the xerothermic thicket *Peucedano-Coryletum*, two forest communities: *Tilio-Carpinetum* and *Fraxino-Ulmetum*, and several other plant communities (KĘPCZYŃSKI, ZAŁUSKI 1982) (Fig. 2). Bees were studied at this site in 1975−1977 (BANASZAK 1980) and in 2000.

2. Raciążek near Ciechocinek (UTM CD56). The study site includes extensive xerothermic swards and tall-herb communities (with *Anchusa officinale, Ballota nigra, Chelidonium maius, Cichorium intybus, Trifolium pratense, Salvia pratensis, Medicago falcata*) on slopes with southwestern exposures and slope angle of about 45º. The site was visited only once in 1975 (BANASZAK 1975, 1980).

3. Ciechocinek (UTM CD55). Observations were made in grassland communities covering flood embankments near the Vistula. The site was visited only once in July 1975, when the Apiformes collected pollen from abundantly flowering *Anchusa officinalis*, particularly attractive for numerous bumblebees (Banaszak 1975, 1980).

4. Otłoczyn near Toruń (UTM CD46). Investigations were carried out in July 1975 on a mid-forest sand dune located near the small railway station. Bees were collected from flowers of *Centaurea rhenana* and *Thymus* sp., which were abundant there (BANASZAK 1975, 1980).

5. Łęgnowo near Bydgoszcz (UTM CD08). Investigations were conducted in May–July 1971 on slopes of the Vistula valley with southern exposure, near the small railway station.

6. Bydgoszcz-Fordon (UTM CD09). The research site is the southern part of the Fordon Valley. The slope was dominated by grassland communities with numerous bee forage plants, e.g. *Potentilla* spp., *Fragaria vesca*, *Melilotus officinalis*, *Myosotis* spp., *Senecio* spp., and *Salvia pratensis*. Shrubs covered about 25% of the site and included *Crataegus monogyna*, *Rosa canina* and single specimens of *Syringa vulgaris*. No tree layer developed on the slope and there were no sandy walls. On the plateau above the slope, a patch of fallow land accompanied a neglected farmstead. On the terrace below the slope, a large housing estate is located, composed of apartment bocks. Bees were collected in 1998−2001 on the slope with western and southern exposures (Fig. 3).

7. Strzelce Dolne (UTM CE10). The study site is situated in the central part of the Fordon Valley, on the left bank of the Vistula. Because of the small height and the neighbouring village, meadows and pastures covered the slope. They were dominated by grasses, but some patches of bee forage plants were found, mainly near the village. These included mainly *Melilotus officinalis*, *Vicia sepium*, *V. cracca*, *Cirsium arvense*, *Coronilla varia*, *Malva* cultivars, and several specimens of *Dipsacus sylvestris*. Shrubs and trees occurred there singly. In the year 2000, field research was conducted on a barrow and the nearby slope of the valley.

8. Reserve 'Kozielec' (UTM CE10). The slope is located in the central part of the Fordon Valley. The main plant association was *Adonido-Brachypodietum pinnati* with its intermediate forms gradually overgrown by shrubs of the class *Rhamno-Prunetea* (KRASICKA-KORCZYŃSKA ET AL. 1995). The shrub layer was represented by single specimens of *Crataegus monogyna* and *Rosa canina*. A sandy wall of 0.5-2.5 m in height extended over a distance of several dozen metres. The neighbouring plateau was covered with a cereal field, while the flood plain by a potato field and a meadow. Bees were collected there in 2000–2002 on the slope with southern and eastern exposures (Fig. 4).

9. Unisław (UTM CD29). The site is located in the central part of the Fordon Valley. Slope degree reached there 45º. The slope was covered by grassland of the class *Festuco-Brometea*. Bee forage plants were represented there by *Potentilla arenaria* Bork, *Salvia pratensis*, *Adonis vernalis*, and *Campanula sybirica*. The site was visited twice in 2000, and samples were collected on the slope with western exposure.

10. Reserve 'Zbocza Płutowskie' (UTM CE20). Samples of Apiformes were collected on high (60 m) slopes with western and southern exposures, on slopes of the Vistula valley between the villages of Płutowo and Starogród and in the adjacent erosional ravines. The steep slopes are covered by well-developed patches of herbaceous associations *Potentillo-Stipetum* and *Adonido-Brachypodietum* as well as shrub associations *Peucedano*-Coryletum and Prunus spinosa. In 1963 the slopes between the Płutowo Ravine and Starogród started to be protected as a nature reserve. Since then, shrubs and trees have been gradually colonizing the slopes, so that now only 30–60% of the protected area are occupied by xerothermic herbaceous communities. Research on Apiformes was conducted there in 1972 and 1975 (BANASZAK 1975, 1980), but also in 1991–1992 and 1999.

11. Kiełp near Chełmno (UTM CE20). The largest of the ravines crossing the reserve 'Zbocza Płutowskie' extends over a distance of 1.5 km towards the village of Kiełp. On the southern slopes of the ravine, bees were collected in August 1971 (BANASZAK 1970, 1980).

12. Starogród near Chełmno (UTM CE21). This is an extension of the xerothermic sward whose northern part is protected as the reserve 'Zbocza Płutowskie'. The dominant association was *Adonido-Brachypodietum* and thickets of the class *Prunetalia*. Apiformes were studied there in 1971 (BANASZAK 1980).

13. Reserve 'Góra Św. Wawrzyńca' near Chełmno (UTM CE21). This is a partly manmade hill located north of the village of Starogród. Its southeastern part of 0.75 ha was covered by xerothermophilous plants of the association *Potentillo-Stipetum*, protected as a nature reserve from 1962. Bees were studied there in August 1971 (BANASZAK 1975, 1980).

14. Reserve 'Gruczno' (UTM CE21) lies in the southern part of the Fordon Valley, on the left bank of the Vistula. The reserve occupies the edge of the Vistula valley, with relative height of about 40 m and slope degree of 15–30º. The slope is dissected by numerous ravines (Fig. 5). The slope surface is generally well-preserved but in many places it is eroded and sandy or clayey escarpments have been formed. The main type of bedrock of the soils in the reserve is sand, often between clay layers.

The diverse relief of the reserve creates suitable conditions for species from many ecological groups (CEYNOWA-GIEŁDON, WALDON 2001). Well-developed xerothermic plant communities covered extremely xerothermic sites. This group included 10 plant communities, e.g. *Potentillo-Stipetum capillatae* and *Brachypodium pinnati* (the latter similar in composition to *Adonido-Brachypodietum*, but with fewer steppe species). Besides, many communities of the phytosociological classes *Artemisietea*, *Molinio-Arrhenatheretea* and *Trifolio-Geranietea sanguinei* were found there. No forest communities proper had developed in the reserve. There were only shrub communities and small patches of open forest (degree of cover by the tree layer <50%) in more moist erosional sections. The tree layer was dominated by *Populus alba* and *P. tremula*, with some oaks (*Quercus robur* and *Q. sessilis*), *Acer pseudoplatanus, A. platanoides, Tilia cordata*, and *Pinus sylvestris*. The shrub layer was composed mainly of *Crataegus* monogyna, Cornus sanguinea and Prunus spinosa. Distribution of main types of vegetation in the reserve is presented in Fig. 6. Earlier research was conducted in 1972 and 1973 (BANASZAK 1975, 1980). New data on Apiformes were collected in this reserve in 1999–2001.

This study site needs to be characterized in greater detail because five plots were distinguished in the reserve, to analyse the variation in species composition and structure of bee communities within this research site (Fig. 6):

Plot A is located in the southern part of the reserve, with slope degree of 20º and southern exposure. It was a patch of xerothermic grassland *Potentillo-Stipetum capillatae*, with degree of cover of 80–100%. Tufts of the dominant *Stipa joannis* were interspersed with some species resistant to drought and high temperatures, e.g. *Potentilla arenaria*, *Medicago falcata*, *Centaurea stoebe*, *Fragaria viridis*, *Coronilla varia*, *Medicago lupulina*. Within the radius of 100 m from the traps, there were small patches of open forest, thickets of the class *Rhamno-Prunetea*, xerothermic edge communities of the class *Trifolio-Geranietea*, and a patch with *Calamagrostis epigejos*. On the neighbouring plateau, cereals were cultivated.

Plot B is situated in a gap between patches of open forest, on a slope with southern exposure and angle of 15–40º. It was covered by the xerothermic sward community *Potentillo-Stipetum capillatae*, communities dominated by *Calamagrostis arundinaceus*, *Centaurea rhenana* or *Brachypodium pinnatum*, and communities intermediate between *Festuco-Brometea* and *Sedo-Scleranthetea*. The ecotone zones between them and the neighbouring wooded patches were occupied by xerothermic thickets of the class Trifolio-Geranietea and a community with Prunus spinosa. The mean degree of cover by the herb layer was 90%. The vicinity of the plot was dominated by patches with *Betula pendula* and *Populus alba*. Under the scarce canopy of widely spaced trees there were some bushes of *Cornus sanguinea*, *Crataegus monogyna*, *Corylus avellana*, *Rosa canina* and *R. rubiginosa*. In a place where water was seeping through the ground, a patch of *Phragmites australis* had developed.

Plot C is located on a slope with southern exposure and angle of 0–5º. Traps were placed at the border between the synanthropic plant community *Tanaceto-Artemisietum* and xerothermic and sandy swards (communities with *Brachypodium pinnatum*, *Calamagrostis epigejos*, *Phleum phleoides*). Apart from the dominant grasses, only infrequent bee forage plants were found there: *Potentilla arenaria*, *Centaurea stoebe*, *Medicago falcata*, *Fragaria viridis*. The degree of cover by the herb layer amounted to 80%. Nearby there were some cereal fields.

Plot D is located on a slope with southern exposure and angle of 45º. Traps were placed at the border of a thicket dominated by *Rubus caesius*, with relatively high contributions of meadow species, including bee forage plants: *Medicago falcata, Salvia pratensis, Centaurea stoebe, Pimpinella saxifraga,* and *Potentilla arenaria*. The neighbourhood was dominated by synanthropic communities of the class *Artemisietea vulgaris* (community with *Bromus inermis* or with *Melilotus* spp.), xerothermic shrub communities of the class *Trifolio-Geranietea*, and a community with *Calamagrostis epigejos*. At the top of the slope, the plot bordered on arable fields.

Plot E is situated in the lower part of the slope, with eastern exposure and angle of 30º. Traps were placed in a plant community with *Bromus inermis* and *Artemisia campestris*. It was an initial community characterized by a relatively low degree of cover by vegetation (80%). The dominant *Artemisia campestre* and *Phleum phleoides* were accompanied by *Centaurea stoebe*, *Veronica spicata*, *Medicago falcata*, and *Hypericum perforatum*. The plot was surrounded by shrub communities of the class *Rhamno-Prunetea*, xerothermic grassland of the class *Rhamno-Prunetea* and communities with *Calamagrostis arundinaceus*. The eastern part of the plot bordered on a village with ruderal communities and gardens.

15. Świecie (UTM CE32). The slope is located in the southern part of the Grudziądz Basin and is characterized by a large relative height (about 50–60 m) and slope angle of up to 60º. The xerothermic sward includes many bee forage plants, such as *Campanula sibirica*, *Melilotus officinalis*, and *Anthemis tinctoria*. The plot was surrounded by shrubs, mainly *Crataegus monogyna*, *Rosa canina*, *Symphoricarpos albus* and single trees, particularly *Carpinus betulus*. Sandy walls, about half a metre high and several metres long, were largely covered by vegetation. Bees nested in exposed, sandy fragments of the slope. The upper part of the slope bordered on a meadow. The terrace at the foot of the slope was covered by pastures with single farmsteads. Samples were collected in 1998–2001 on the slope with eastern exposure.

16. Nowe (UTM CE54). The site is located in the Kwidzyn Valley, on the left bank of the Vistula, near the town of Nowe. It is characterized by a large relative height of 70 m and slope angle of up to 50°. The area was dominated by grassland with numerous bee forage plants: *Taraxacum officinale*, *Potentilla* spp., *Cirsium arvense*, *Melilotus officinalis*, *Myosotis* spp., *Senecio* spp., *Salvia pratensis*, and *Echium vulgare*. In the summer period, the dominant bee forage plant was *Solidago canadensis*, which in some places formed dense patches of several hundred metres square. Another species occupying a large proportion of the area was Tanacetum vulgare, found mainly in an extensive patch on the plateau above the slope. The shrub layer was represented by small groups or single specimens of *Crataegus monogyna* or clumps of *Rosa canina*, accounting for up to 5% of the area (Fig. 7). Bees were caught there in 2002 on the xerothermic grassland covering the slope and on the plateau above it, extending over more than 500 m and gradually replaced by forest.

17. Reserve 'Biała Góra' near Sztum (UTM CE67). This is the northernmost of the studied localities with xerothermic vegetation. Since 1968 it has been protected as a reserve. Bees were studied on a high slope (up to 60 m) with southern exposure. The slope was covered by xerothermic grassland forming a mosaic of various communities of the class *Festuco-Brometea* with some rare steppe species. The protected slope was gradually colonized, mainly from the south and west, by shrubs (*Crataegus* spp.) and trees (*Pinus sylvestris*, *Populus tremula*) (Fig. 8). Fourteen bee species were recorded there in July 1972 and 1975 (BANASZAK 1975, 1980). New sampling sessions were carried out in 2002.

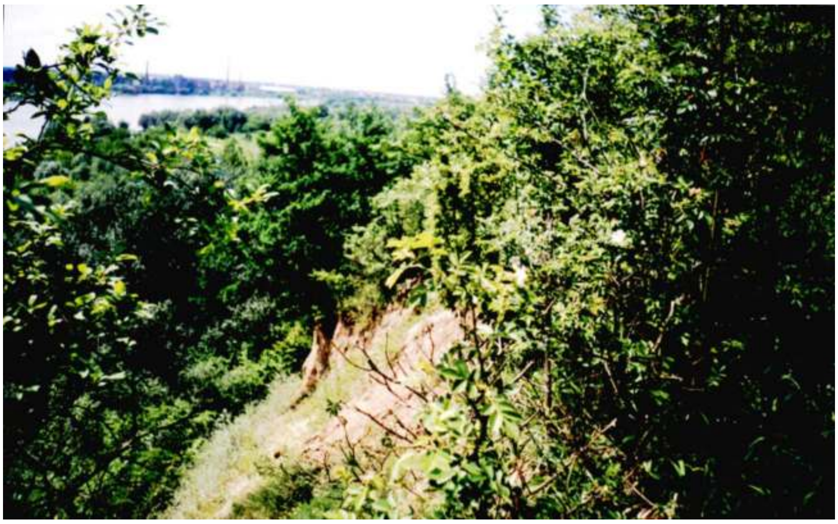

Fig. 2. Reserve 'Kulin', with a large contribution of shrubs. Photo by H. RATYŃSKA.

Fig. 3. Bydgoszcz-Fordon: open slope of the Vistula valley with a view of Bydgoszcz city. Photo by J. BANASZAK.

Fig. 4. Reserve 'Kozielec': slopes of the Vistula valley, with an exposed sandy wall. Photo by R. KRIGER.

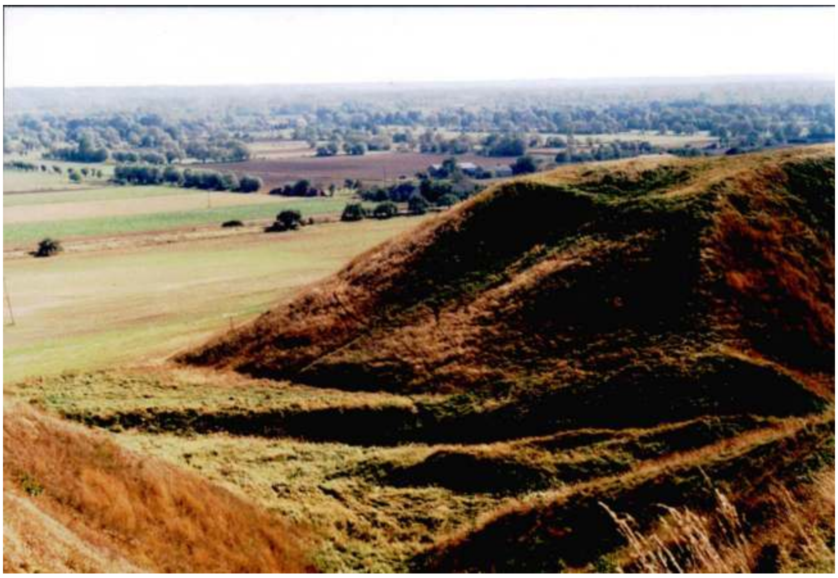

Fig. 5. Reserve 'Gruczno', with well-developed patches of xerothermic vegetation and a view of the Vistula valley. Photo by B. WALDON.

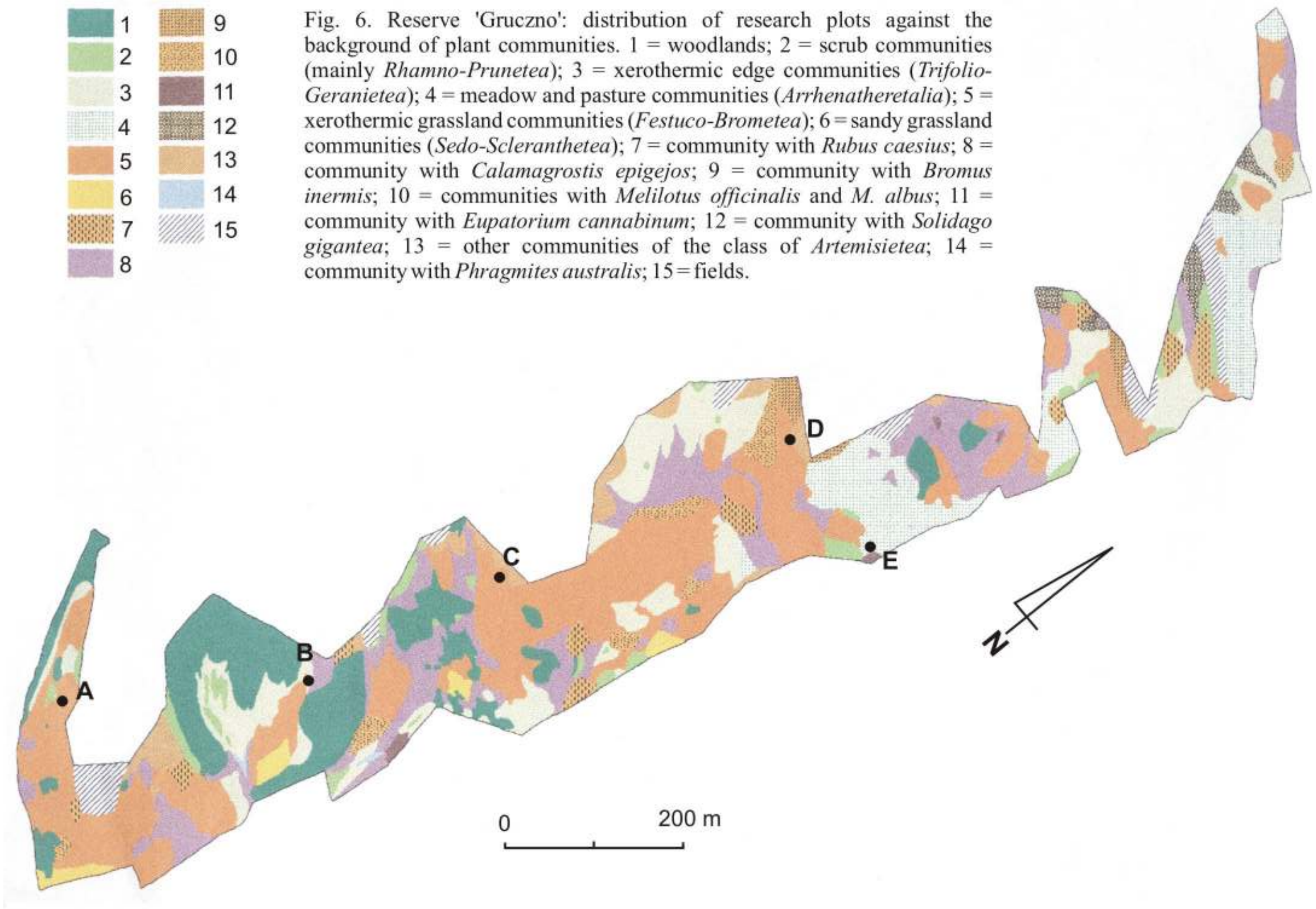

Fig. 6. Reserve 'Gruczno': distribution of research plots against the background of plant communities. 1 = woodlands; 2 = scrub communities (mainly *Rhamno-Prunetea*); 3 = xerothermic edge communities (*Trifolio-Geranietea*); 4 = meadow and pasture communities (*Arrhenatheretalia*); 5 = xerothermic grassland communities (*Festuco-Brometea*); 6 = sandy grassland communities (*Sedo-Scleranthetea*); 7 = community with *Rubus caesius*; 8 = community with *Calamagrostis epigejos*; 9 = community with *Bromus inermis*; 10 = communities with *Melilotus officinalis* and *M. albus*; 11 = community with *Eupatorium cannabinum*; 12 = community with *Solidago gigantea*; 13 = other communities of the class of *Artemisietea*; 14 = community with *Phragmites australis*; 15 = fields.

Fig. 7. Nowe: steep slope with relative height of 70 m and angle of up to 50°. Photo by J. BANASZAK.

Fig. 8. Reserve ‘Biała Góra’ near Sztum: northernmost research site. Photo by J. BANASZAK.

MATERIAL AND METHODS

This work is based on entomological material collected at the 17 xerothermic sites presented above (Fig. 1). At 11 of the sites, research was conducted in 1998–2002, including 6 sites (Bydgoszcz-Fordon, Strzelce Dolne, reserve ‘Kozielec’, Unisław, Świecie, Nowe n. Wisłą) in which bees were studied for the first time and the data were not published before. In the case of 5 sites (reserves ‘Kulin’, ‘Zbocza Płutowskie’, ‘Gruczno’, ‘Biała Góra’, and a ravine near Kiełp) we used the original data from 1998–2002 and some earlier published data (BANASZAK 1975, 1980, BANASZAK & CIERZNIAK 1994). For the remaining 6 sites (Raciążek near Torunia, Ciechocinek, Łęgnowo, Starogród near Chełmno, Otłoczyn, reserve ‘Góra św. Wawrzyńca’), material was collected only during BANASZAK’S (1975, 1980) investigations carried out in the 1970s.

During field research, two methods were used: (1) qualitative catches with a sweep net; and (2) quantitative catches with Moericke traps.

Each qualitative sample was taken on a 2–3-hour visit, during which the Apiformes were caught with a sweep net at the given research site. At most of the sites studied in 1998–2002, qualitative samples (Appendix 1) were collected throughout the growing season or – if more frequent sampling was impossible – at least twice, i.e. during the peaks of bee abundance in spring (late April and early May) and summer (July). Qualitative samples were taken at all research sites but numbers of those samples varied between sites (Appendix 1).

Moericke traps were placed at three research sites on the ground surface: 15 in the reserve ‘Gruczno’ in 2001, 3 in Nowe in 2002, and 3 in the reserve ‘Biała Góra’ in 2002. In the reserve ‘Gruczno’, traps were placed in 5 groups of 3 traps each, considering the variation of its plant communities (Fig. 6). In this way, the material collected in this reserve enabled an assessment of the variation in bee communities within this research site. We used white plastic bowls of 20 cm in diameter, filled to 2/3 with an attractant, i.e. mixture of water (95%), ethylene glycol (4.8%) and a detergent (0.2%) decreasing the surface tension. The captured insects were removed from the traps every 7–10 days. Intensity of catches with Moericke traps at individual sites was expressed in trap-days (i.e. number of days multiplied by number of set traps).

Total numbers of bees collected by use of both methods at individual stations are shown in Appendix 1. The caught bees are deposited at the entomological collection of the Institute of Biology and Environment Protection, Kazimierz Wielki University, Bydgoszcz, Poland.

Sampling completeness was assessed by the non-parametric jackknife2 method (BURNHAM, OVERTON 1978, 1979, SMITH, VAN BELLE 1984) and chao2 method (CHAO 1984, 1987). Those methods, in comparison with other parametric and nonparametric methods of estimation of species number in a community, give the best estimates of species richness, i.e. the estimated number of species is the closest to the true number of species in a given community (PALMER 1990, URLICH 1999). The performed tests showed that the best estimates of true number of species are based on the nonparametric estimators jackknife and chao. Jackknife 2 gives good estimates if the collected material includes about 2/3 of the true number of species, because 82% of estimates fit within the range ±10% of the true value (URLICH 1999). The chao2 estimate is less sensitive and gives good estimates in the case of samples where many species are represented by singletons (COLWELL, CODDINGTON 1994), as was the case in our study.

For the plots in the reserve 'Gruczno', we calculated values of the Shannon-Weaver diversity index (SHANNON, WEAWER 1949) and PIELOU evenness index (1975). Significance of differences in the former index was assessed by Hutchinson's formula.

RESULTS

Species diversity and dominance structure of bees in the lower Vistula valley

This work is based on a total catch of 9896 specimens of bees (Apiformes) collected by us on slopes of the valley of the lower Vistula. They were members of 253 bee species, which account for 54.4% of the Polish bee fauna. All species and numbers of specimens caught at individual research sites are listed in Appendix 1.

Sampling completeness was assessed by two methods of estimation of the true number of species: jackknife2 and chao2. The true number of species in the study area was estimated to reach nearly 300 (Fig. 9). This suggests that we recorded about 85% of the true number of species. It is noteworthy that marginal habitats are as a rule foraging sites of many species migrating there periodically from the river floodplain (meadows, fields) or from the plateau (ruderal communities, fields). Partly for this reason, numbers of recorded species varied in time, so the total number of species can be only roughly estimated.

Seasonal variation was observed in species composition, diversity and abundance of the studied bee communities. Starting from late March, numbers of early spring species increased quickly. The most typical and abundant species of this group were: *Colletes cunicularis, Andrena barbilabris, A. vaga, A. haemorrhoa, A. praecox, Anthophora acervorum,* etc. In late April, as many as 90 species were recorded in the study area. In early May, the early spring species disappeared and were gradually replaced by spring species. The latter group was the most diverse in late May and early June, when over 100 species were recorded. In mid-June, bee diversity fell rapidly to 30 species. Afterwards, summer species emerged, and another peak in diversity (over 100 species again) was recorded in early August. From mid-August, numbers of bee species decreased dramatically. The seasonal variation in numbers of bee species and individuals is presented in Fig. 15.

The dominant group of Apiformes in the study area were the Halictidae (Fig. 10). This was particularly conspicuous in the steppe reserve 'Gruczno', which was the best studied (50% of total catch) and, consequently, reflected to the greatest extent the relationships in xerothermic communities (Fig. 11). Halictid bees accounted for 27% of the total number of species recorded in the lower Vistula valley, compared to 34% in the reserve 'Gruczno' and 23% in Poland. Thus they are highly dominant in xerothermic communities. By contrast, the Megachilidae and Anthophoridae were less diverse there than generally in Poland (Figs. 10 and 12).

The dominant bee species in the study area was *Evylaeus morio,* which accounted for 14.3% of the total catch. Subdominants included *Andrena flavipes* (9.5%), *Evylaeus pauxillus* (6.6%), *E. linearis* (6.0%), *Andrena vaga* (5.2%), *Seladonia tumulorum* (3.4%) and *S. subaurata* (3.3%) (Fig. 12).

The group of dominant and subdominant species had the same composition only at some sites ('Gruczno', 'Zbocza Płutowskie', Świecie), while in other sites it was markedly different. This was associated with differences in the areal ratio of xerothermic grassland to other plant communities. As the area of grassland decreased and the area covered by thickets, forest, or other communities increased, a decline was observed in the proportion of xerothermophilous species of the genera *Evylaeus* (*E. morio*, *E. pauxillus*, *E. linearis*) and *Seladonia* (*S. tumulorum, S. subaurata*). They were replaced by more eurytopic species (e.g. *Hylaeus communis*, *Anthophora plumipes*, *Andrena haemorrhoa*). This is clearly illustrated by the comparison of dominance structures of bees in the steppe reserve 'Gruczno' and in the reserve 'Biała Góra', which is gradually overgrown by shrubs and forest (Figs. 13 and 14).

Evylaeus morio, which dominated in xerothermic communities, is the most common member of the genus in Europe (where it reaches latitudes of up to 60º) and in North Africa. It prefers open habitats, as it is more abundant in steppes and dry meadows than in wooded habitats. It nests in warm, dry, and open habitats. It is primitively eusocial, forming large nesting colonies. Thus our data from the Vistula valley confirm the earlier published data (PESENKO ET AL. 2000).

Other halictids of the subdominant group, i.e. *Evylaeus pauxillus, E. linearis* and *Seladonia tumulorum*, are species common in Poland, primitively eusocial, preferring flowers of the Asteraceae. They have similar ecological preferences, as they also colonize dry grasslands, slopes, and other dry and warm sites. Also the clearly xerothermophilous *Seladonia subaurata*, although infrequent in Poland, was common on slopes of the lower Vistula valley.

The high contributions of two andrenid species in the group of subdominants is relatively easy to explain. Both species are common in Poland and find favourable nesting and foraging sites on slopes of the Vistula valley. *Andrena flavipes* is eurytopic, occurring in dry and moist sites, and is also widely oligotrophic. *A. vaga* is an early spring species, nesting in large or very large aggregations at dry sites, such as sandy banks. It collects pollen chiefly from flowering willows and sallows (*Salix* spp.), whose thickets are common on the river floodplain, or from dandelion (*Taraxacum officinale.*), which are abundant on the local meadows.

The above bee species should be also considered characteristic for the lower Vistula valley, as they are numerous and found regularly at all or nearly all research sites.

A commentary on *Halictus simplex* and *H. compressus* is needed here. In his first report from the Vistula valley, BANASZAK (1980) distinguished *H. simplex* as characteristic for xerothermic grassland. At present we are more cautious when identifying this species, i.e. we can reliably identify only males of *H. simplex,* while females of both species of the subgenus *Monilapis* COCKERELL – namely *H. simplex* BLŰTHGEN, 1923 and *H. compressus* (WALCKENAER, 1802) – are virtually indistinguishable (PESENKO et al. 2000). Occurrence of the latter species has been confirmed in southern Poland, although only on the basis of males. *H. simplex* is infrequent but recorded in all regions of Poland. The earlier BANASZAK'S (1980) opinion that *H. simplex* is a characteristic species for the study area, can be maintained on the basis of its occurrence nearly exclusively in xerothermic sward.

Despite intensive investigations in the extensive study area, only single individuals of many species were caught. The group of 70 rare species (1–3 individuals caught) accounted for 27.4% of the total number of recorded species, and among them 41 species were represented by single individuals (Appendix 1). Some of them are rare in Poland for zoogeographic reasons and those species are discussed in detail in the next section. Some species are included in the Polish *Red List of Threatened and Endangered Animals* (BANASZAK 2002). Many of them are regarded as vulnerable (VU) in Poland: *Hylaeus punctatus, Andrena nasuta, A. nycthemera, A. suerinensis, A. symphyti, Nomioides minutissimus, Anthophora pubescens,* and *Bombus subterraneus.*

Many bee species found in the lower Vistula valley are rare species of indeterminate status (DD): *Duforuea inernis*, *Evylaeus interruptus*, *E. nigripes*, *Sphecodes ruficrus*, *S. spinularus*, *Hoplitis tridentata*, *Nomada fulva*, *Hylaeus bisinuatus*, and *H. moricei*. Some of the species that were rare in the study area are common in Poland, e.g. Chalicodoma ericetorum, Megachile willughbiella, M. maritima, and M. lagopoda.

It is noteworthy that the abundance of bumblebees was very low in the study area. We recorded 16 bumble bee species and they accounted for only 4.8% of the total catch (the most abundant among them, *Bombus lapidarius*, accounted for 1.1%).

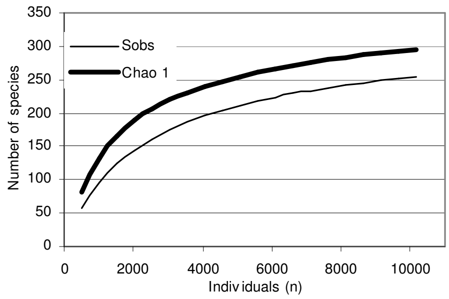

Fig. 9. Observed and estimated numbers of species of bees (Apiformes) in xerothermic plant communities of the lower Vistula valley.

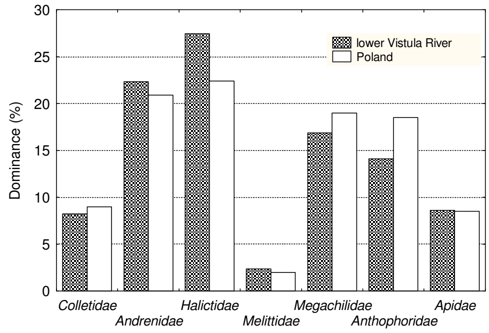

Fig. 10. Comparison of contributions of bee families to the total number of species of Apiformes in xerothermic communities of the lower Vistula valley and in Poland.

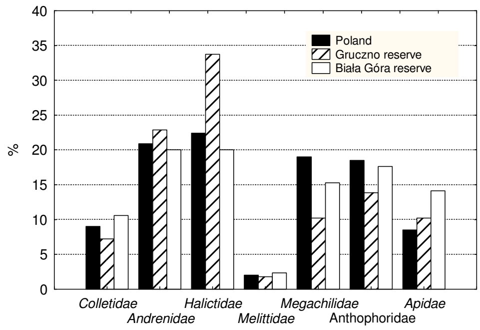

Fig. 11. Comparison of contributions of bee families to the total number of species of Apiformes in xerothermic communities of reserves 'Gruczno' and 'Biała Góra' and in Poland.

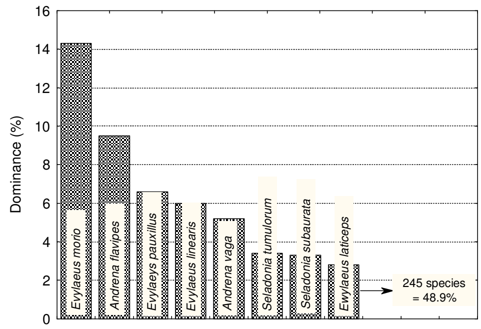

Fig. 12. Dominance structure of bees (Apiformes) in xerothermic communities in the lower Vistula valley.

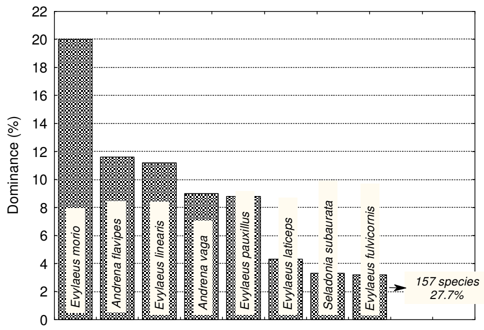

Fig. 13. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Gruczno'.

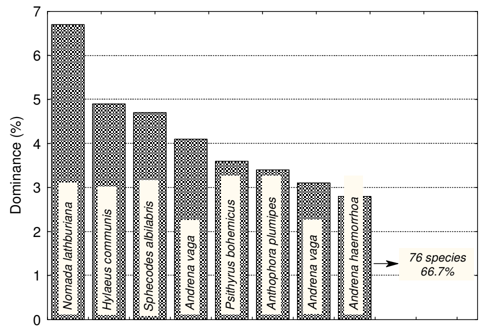

Fig. 14. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Biała Góra'.

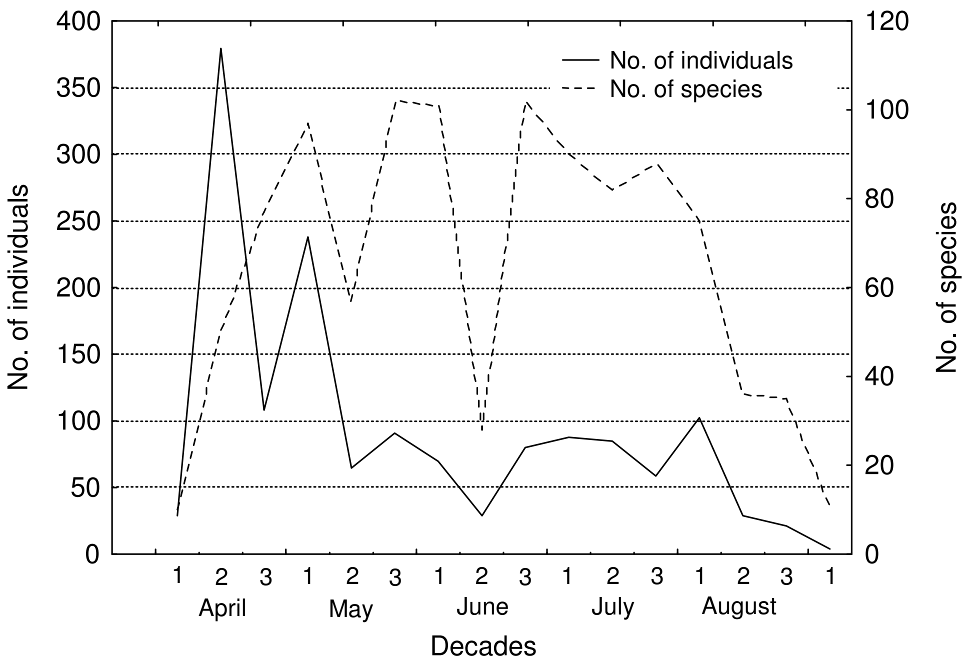

Fig. 15. Dynamics of abundance and diversity of bees (Apiformes) in xerothermic communities of the lower Vistula valley.

Assessment of faunistic distinctness of individual sites

At some of the studied sites our investigations were much more intensive than at other sites, so their faunistic similarity cannot be assessed. Bees were collected with a sweep net at all sites, but numbers of samples and total time of sampling sessions varied. Moericke traps were used only at sites 9, 16 and 17. Results from all sites reflect the total bee fauna of xerothermic grasslands in the lower Vistula valley.

Despite methodological reservations, it seems that material collected at eight sites allows us to attempt an assessment of faunistic differences between them. The richest material, enabling a reliable faunistic characterization, was collected in the reserve 'Gruczno' (site 14: 5195 bees). Satisfactory material was also available for the reserve in reserves 'Kozielec' (site 8: 867 bees), 'Zbocza Płutowskie' (site 10: 930 bees), Świecie (site 15: 830 bees), and Nowe (site 16: 621 bees). Lower numbers were recorded in Bydgoszcz-Fordon (site 6: 389 bees) and reserves 'Biała Góra' (site 17: 386 bees) and 'Kulin' (site 1: 234 bees).

At the sites mentioned above, also relatively large numbers of bee species were found, as compared to the total of 253 recorded species of Apiformes in the lower Vistula valley: 165 species in 'Gruczno' (14), 114 in Bydgoszcz-Fordon (4), 108 in 'Kozielec' (6), 125 in 'Zbocza Płutowskie' (8), 87 in Świecie (6), 98 in Nowe (16), 85 in 'Biała Góra' (17), and 81 in 'Kulin' (1). The above data show that the collected material was sufficient, because higher numbers of caught individuals at some sites were not associated with higher numbers of species. For example, in Świecie (10) and the reserve 'Biała Góra' (12), similar numbers of species were found (87 and 85, respectively) although over twice as many individuals were caught in Świecie than in 'Biała Góra'.

The values listed above suggest that the material from those sites enables their satisfactory faunistic characterization. This, in turn, prompted us to compare their dominance structures, shown in Figs 16-21. The dominance structure for the whole material (described in the previous section) was representative of the structure of the bee community in xerothermic grasslands in 'Gruczno' and also in Świecie, where *Evylaeus morio* dominated (>30%) with other halictids (Fig. 21). However, the dominance structures at other sites were surprisingly distinct. This was due to the local environmental conditions. For example, the presence of clayey or sandy walls with favourable nesting sites was probably the main cause of the dominance of *Colletes daviesancus* (≈10%) in 'Kulin' (Fig. 16) or *Andrena flavipes* (≈ 23%) in 'Kozielec' (Fig. 18).

It can be concluded that the faunistic distinctness of individual sites results from differences in environmental conditions, e.g. the substrate (sand, clay), land relief (slopes, banks), dominant plant community, area covered by the community, and – to a lesser extent – geographic location (e.g. 'Kulin' versus 'Biała Góra').

The above analyses were somewhat biased because of methodological differences, so they might not seem to reflect true and significant differences between the studied bee communities in the lower Vistula valley. More convincing results were provided by the use of Moericke traps in 5 microhabitats in the reserve 'Gruczno'. The applied method enabled a reliable comparison of variation in composition and dominance structure of bee communities under the influence of various plant communities and land relief, in the seemingly uniform biotope of Vistula valley slopes in this reserve. The whole reserve (about 1400 m × 100 m) was divided into 5 plots (A, B, C, D, E) of similar size (about 3 ha each). The plots differed in slope angle, flora, plant communities, and degree of cover by vegetation (Fig. 6). In the central part of each plot, the same number of Moericke traps was set (see Material and Methods). Table 1 shows that the plots greatly differed in bee diversity. In the whole reserve, a total of 165 bee species were caught, but numbers of species recorded on individual plots varied from 20 to 78, so the respective diversity indices ranged from 2.7 to 3.3. The example of 'Gruczno' clearly confirms how strongly the fauna is affected by environmental factors, such as land relief, substrate (sand, clay) or microclimate. Most species were caught on plots A and E, with infrequent but diverse shrubs, many bee forage plants, r patches of ruderal vegetation. Plot C, where only 20 bee species were found (H' = 2.1), was a slope dominated by grasses, with infrequent bee forage plants, and accompanied only by cereal fields. The studied plots differ also in bee dominance structures (Fig. 22 and 23). It is noteworthy that the remarkable differences in taxonomic composition and dominance structure mentioned above concern sites located only 200–300 m apart.

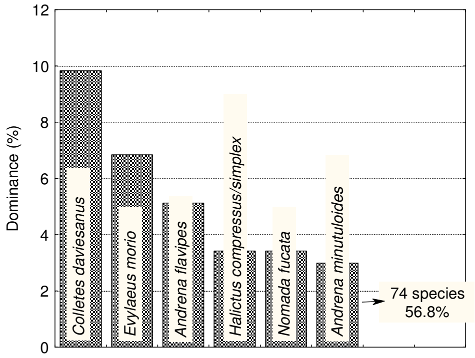

Fig. 16. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Kulin'.".

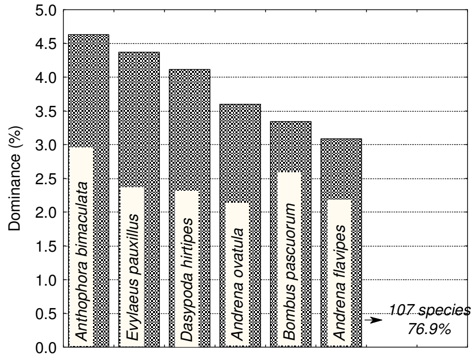

Fig. 17. Dominance structure of bees (Apiformes) in xerothermic communities in Bydgoszcz-Fordon.

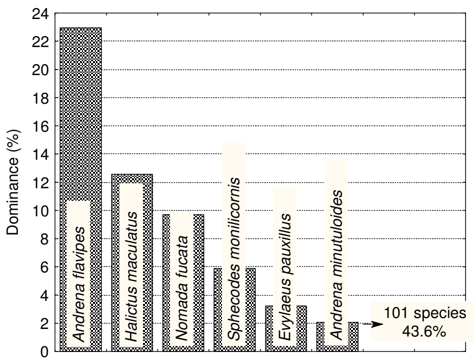

Fig. 18. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Kozielec'.

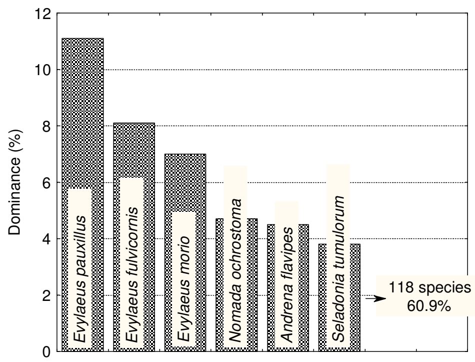

Fig. 19. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Zbocza Płutowskie'.

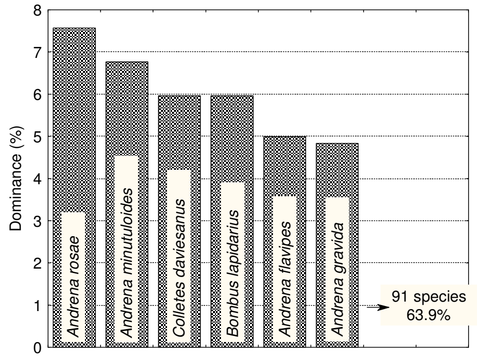

Fig. 20. Dominance structure of bees (Apiformes) in xerothermic communities in Nowe.

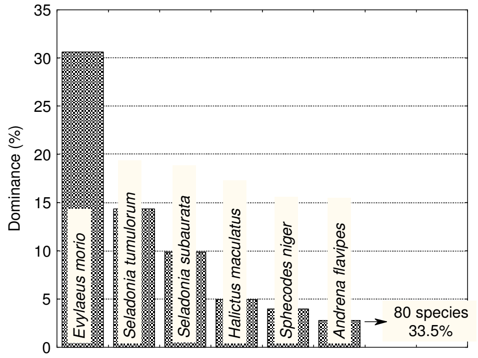

Fig. 21. Dominance structure of bees (Apiformes) in xerothermic communities in Świecie.

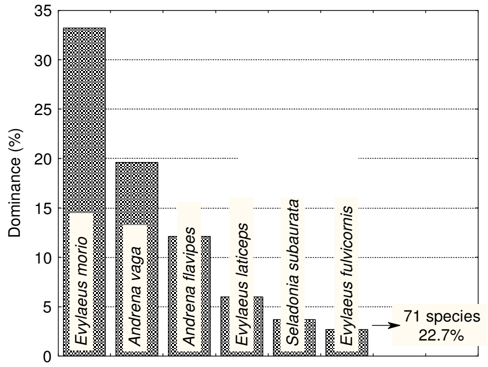

Fig. 22. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Gruczno' on plot A.

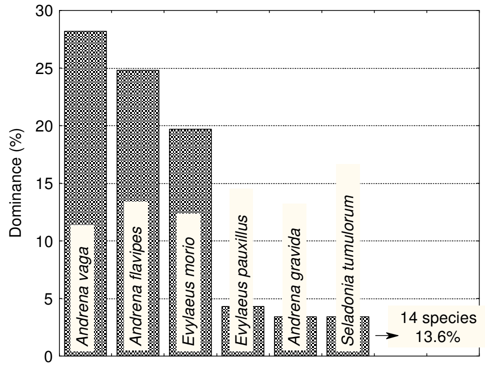

Fig. 23. Dominance structure of bees (Apiformes) in xerothermic communities in the reserve 'Gruczno' on plot C.

Table 1. Comparision of number of species (S), species diversity index (H') and evennes index (J') of bees (Apiformes) in the reserve „Gruczno" on plots (A-E).

Plot / Index	A	B	C	D	E
H`	2.549	2.564	2.168	2.958	3.341
J`	0.585	0.604	0.724	0.732	0.781
S	78	70	20	57	72

ZOOGEOGRAPHIC CHARACTERISTICS OF THE BEE FAUNA

Among the bee species recorded in the lower Vistula region, 13 zoogeographic elements can be distinguished. It is not surprising that at this latitude most species (54.4%) are widely distributed: Holarctic, Palaearctic (including West Palaearctic) or Euro-Siberian, and that there are substantial contributions of European (11.9%) or Euro-Caucasian species (5.5%). Northern and central parts of Europe are represented by 7 species (2.8%). Slopes of the Vistula valley are also visited by one boreal species, i.e. *Bombus semenoviellus*. It was recorded for the first time only 10 years ago in Poland, but now it occurs nearly throughout Poland, mainly on meadows. It is noteworthy that another species recorded in the study area − *Andrena fulva* − is also expansive. This distinctly West European bee was recorded only west of the Vistula river till the 1970s (BANASZAK 1982), but its range has extended eastwards nearly to the eastern borders of Poland (BANASZAK 2003).

A characteristic feature of the studied fauna is the participation of southern and south-eastern species, whose centres of distribution lie in basins of the Mediterranean and Black Sea. These are mainly Ponto-Mediterranean species as defined by Holdhaus (after KUNTZE and NOSKIEWICZ 1938), which are widely distributed in southern Europe, spreading in the west to France and Spain, northwestern Africa, in the north to southern Poland and central Germany, and in the east to southwestern Siberia. This group inhabits much of the areas surrounding the Mediterranean Sea and the Black Sea. Some species, however, are of more eastern origin, so they were treated here as Pontic (after the same authors). The western limit of Pontic elements is described by those authors as follows: Lower Austria, the Balkan Peninsula, eastern Małopolska (SE Poland). Also a group of Mediterranean and sub-Mediterranean species was distinguished here. They are closely associated with the Mediterranean Sea, although spreading to the western shores of the Black Sea, as presented by KOSTROWICKI (1953). In contrast to KUNTZE and NOSKIEWICZ'S (1938) suggestion, we do not consider sub-Mediterranean elements as equivalent to Ponto-Mediterranean.

The southern taxa in the bee fauna of xerothermic grasslands of the lower Vistula represent mainly the Ponto-Mediterranean element (30 species, i.e. 12% of all recorded taxa). Ten species (4%) are Pontic or sub-Pontic, while eight taxa (3%)are Mediterranean or sub-Mediterranean.

The comparison of southern zoogeographic elements in individual reserves is impossible because they are very rare. Their contribution to the total catch is negligible, as usually only single or very few specimens were caught, so their detection is a matter of chance. For example, the steppe species *Andrena paucisquana* was recorded only in two reserves on both sides of the river: 'Zbocza Płutowskie' (2 individuals), and 'Kozielec' (2 individuals). Thus in all probability this species occurs also in the neighbouring reserves, such as the best-studied 'Gruczno', although it was not recorded there.

ORIGIN OF THE BEE FAUNA

Botanists assume that there are two major routes of migration of xerothermic plants to Pomerania during late glacial and postglacial times: along the Toruń-Eberswalde Proglacial Valley from the refuge in central Germany and along the Vistula river from the refuge in the Podolye region (part of Poland before the 2nd World War, now in western Ukraine). DZIUBAŁTOWSKI (1934) supposed that the Vistula valley was the major migratory route for the steppe vegetation of the lower Vistula valley, whereas PREUSS (1912) suggested that after the last glaciation the first steppe plants migrated there from the west, along the Toruń-Eberswalde Proglacial Valley. A similar view was expressed by CZUBIŃSKI (1950) and many modern botanists. Opinions of zoologists are varied, too. BUSZKO (1990) describes two possible routes of the spread of xerothermophilous species of mining butterflies in Poland: from the west along the Noteć river to the lower Vistula river, and from the south across the Moravian Gate to the upper Vistula and Oder rivers. Research conducted by LIANA (1973) on Orthoptera provided data on two migratory routes of Acridoidea to the lower Vistula region – from Germany and from the Podolye refuge – but she also mentions the third, Moravian route.

Also the southern bee species could migrate along those three routes to the area of Poland, including the considered lower Vistula region and Pomerania. This view has already been expressed by BANASZAK (1980). We agree with LIANA'S (1973) opinion that the localities from limits of species ranges are the most important for identification of directions of their migrations. Among the species of Apiformes characteristic of xerothermic plant communities, several reach the limits of their geographic ranges in the Vistula valley. Their current distribution seems to attest to their origin clearly. Below we discuss several important examples.

Andrena paucisquama is a steppe species known mainly from the Ukraine, Hungary, Switzerland and the former Czechoslovakia. In Poland it has been reported from Przemyśl, Racławice, the reserve 'Góry Pieprzowe' near Sandomierz (NOSKIEWICZ 1959, BANASZAK 2003) and near Kraków, Stary Sącz and the Pieniny Mountains (DYLEWSKA, NOSKIEWICZ 1963, DYLEWSKA 1974). The reserve 'Zbocza Płutowskie' (site 10) is its northernmost locality. Its distribution suggests that *A. paucisquama* migrated to the lower Vistula valley from the Podolye refuge.

Evylaeus nigripes is a Ponto-Mediterranean species, so in central Europe it is rare, found only in a small number of xerothermic sites. In Germany it was recorded in Thuringia and Saxony. In Poland it has a historical locality in Wrocław (DITTRICH 1903), which is probably no longer valid (NOSKIEWICZ 1959), but has also been reported from Sandomierz, the reserve 'Góry Pieprzowe', and Kazimierz town on the Vistula river (DYLEWSKA, NOSKIEWICZ 1963). The species used to be common in the Podolye region (KUNTZE, NOSKIEWICZ 1938), so it could migrate from there to the lower Vistula region.

Nomioides minutissima also has a historical locality in Wrocław (DITTRICH 1884, 1903), which is probably no longer valid, so that Otłoczyn (site 4) and the Kampinos National Park (BANASZAK 1979) are currently its only known localities in Poland. *N. minutissima* is a sub-Mediterranean, psammophilous species, frequent in the Mediterranean basin but found also in Central Europe: in Hungary and valleys of the rivers Rhein and Main in Germany. KUNTZE AND NOSKIEWICZ (1938) did not record it in the Podolye region, so the species probably migrated to the lower Vistula valley from the western refuges, along the Toruń-Eberswalde Proglacial Valley (Brandenburg-Noteć route).

Heriades crenulatus is a Ponto-Mediterranean species, found in Poland only in Krzyżanowice near Nida, reserve 'Góry Pieprzowe' near Sandomierz (NOSKIEWICZ 1953), Lublin and Chełm Lubelski (ANASIEWICZ 1973), Rogalin near Poznań (BANASZAK 1977), and in the Zamość region (PAWLIKOWSKI, FIJAŁ, KOSIOR 1993). Outside Polish borders it occurs in Saxony and Brandenburg as well as in the Podolye region, so it could migrate to our study area (site 4: Otłoczyn) from both refuges. However, the species is more frequent in the southwestern part of Poland and quite common in the Podolye region, so it probably has migrated from the south along the rivers Vistula or Bug.

Anthocopa bidentata was reported from Poland only once, on the basis of one individual found in 1927 on the left bank of the Vistula, near Puławy (KUNTZE, NOSKIEWICZ 1938; NOSKIEWICZ 1953). This Ponto-Mediterranean species is known in Central Europe from Hungary, Austria, the former Czech Republic, and the Ukraine (Podolye). Thus it probably migrated to our study area (sites 1 and 12: 'Kulin' and Starogród) probably from the eastern refuges, along the Vistula.

Megachile pilidens is also a Ponto-Mediterranean species. Its range extends to the Ukraine (Podolye), the Czech Republic, Slovakia, and Germany (Baden, Saxony, Thuringia and Brandenburg). In Poland it was found before only on 'Góra Wapienna' near Ząbkowice Śląskie (NOSKIEWICZ 1948) and in the reserve 'Góry Pieprzowe' near Sandomierz (NOSKIEWICZ 1953). Its localities in the lower Vistula valley (sites 1, 12, and 14: 'Kulin', Starogród, and 'Gruczno') are its northernmost records. They could be colonized from the west, south, or east, along various routes.

Thus xerothermic swards in the lower Vistula valley – being miniatures of the Ukrainian steppes in floristic terms – are refuges for many southern bee species. The insects could migrate to this area from the east along the Vistula, from the west along the Toruń-Eberswalde Proglacial Valley, or from the south across the Moravian Gate. In our opinion, however, the route along the Vistula prevailed. This is evidenced by the relatively large number of species recorded also in the xerothermic swards along the Vistula near Sandomierz, in the reserve 'Góry Pieprzowe'.

We compiled a list of southern species (Appendix 2) found by various authors in the Podolye region (KUNTZE, NOSKIEWICZ 1938, WIERZEJSKI 1968, 1974, ŚNIEŻEK 1910, NOSKIEWICZ 1922 ab), in the reserve 'Góry Pieprzowe' (BANASZAK 2003) and in the lower Vistula valley. In Podolye, bees were collected on both sides of the Dniester river, mainly on various xerothermic grasslands (so-called *halawy*). In that part of Podolye, 304 bee species were found, and about half of them were southern or southeastern. As reported by NOSKIEWICZ (1922b), this area is very important and distinct in zoogeographic terms because many Mediterranean species and Eurasian species reach their limits there. In his later work, NOSKIEWICZ (1926) listed 73 such species. However, some southern species migrated even further, along the San river towards the Vistula, and colonized slopes of its valley, as evidenced by the rich fauna of the reserve 'Góry Pieprzowe' (BANASZAK 2003). From there, the bees migrated further northwards or spread in the Małopolska region.

However, the analysis of the composition of the 'southern' species collected in the lower Vistula valley shows that majority species probably come from Podolye. Another group is composed of species that are absent from Podolye but are found in the reserve 'Góry Pieprzowe', so they must have migrated to our study area either from the west (e.g. *Andrena lepida, A. niveata, A. suerinensis, Hylaeus punctatus, Evylaeus linearis, E. tarsatus, Osmia mustelina, Megachile rotundata*) (Appendix 2) or from the south, across the Moravian Gate (e.g. *Evylaeus obscuratus*, *Sphecodes cristatus, Andrena assimilis, A. susterai*).

The analysis of the 'southern' fauna also confirms that its diversity declines northwards. KUNTZE (1931), who compared the xerothermic fauna of Podolye with those of Brandenburg, lower Oder river, Lower Austria, and Switzerland, showed clearly that numbers of species (and of higher taxonomic units) decline in the direction from the south to the north. The same applies to the data presented in Appendix 2, which concern latitudes ranging from about 49º (Dniestr river-Podolye) to 53–54º (lower Vistula). Numbers of southern and southwestern species decrease from 165 in Podolye to 48 species (of various origin) in the lower Vistula valley. The contribution of this group to the total number of recorded species also declines northwards: from 50% in Podolye to 32% in the upper Vistula region ('Góry Pieprzowe') and 20% in the lower Vistula valley. This phenomenon is presented graphically in Fig. 24, which takes into account also the rich Moravian refuge of southern bee fauna.

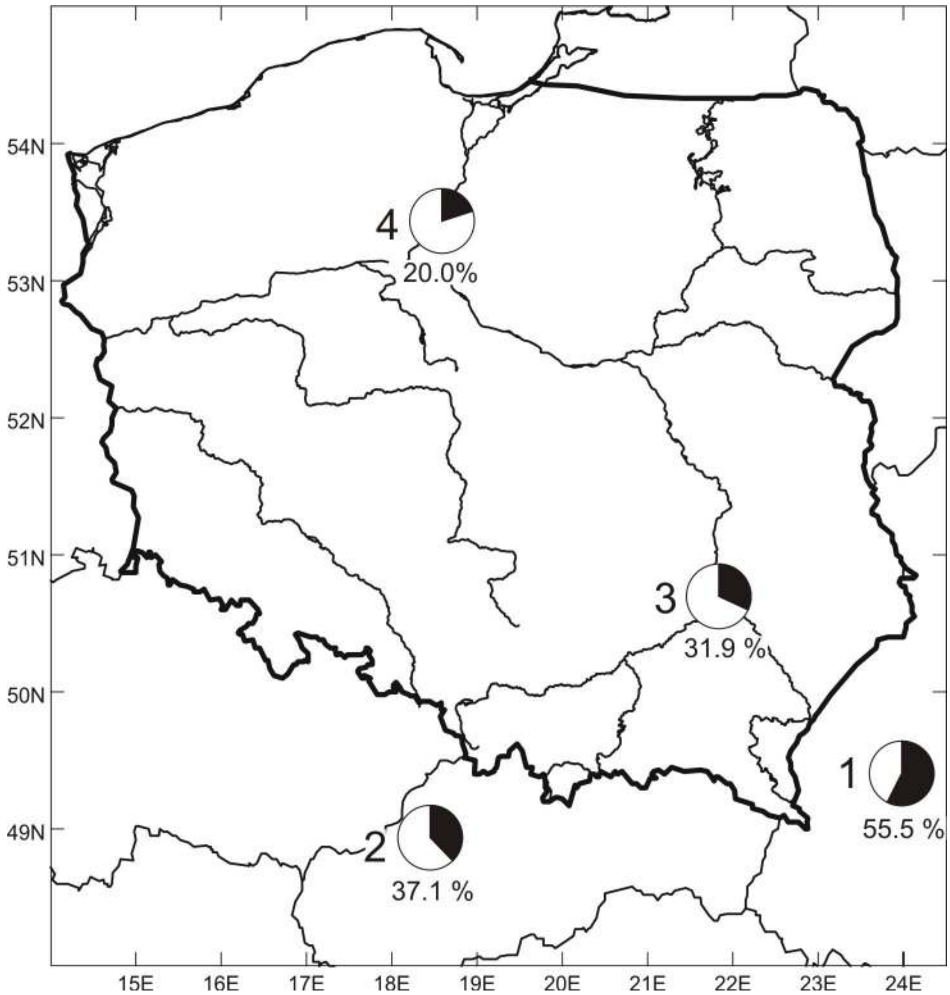

Fig. 24. Contribution of 'southern' species to the total number of species of bees (Apiformes) in xerothermic communities: 1 = Podolye, valley of Dniester and its tributaries (KUNTZE, NOSKIEWICZ 1938, WIERZEJSKI 1968, 1974, ŚNIEŻEK 1910, NOSKIEWICZ 1922 ab); 2 = refuge of xerothermic vegetation Trenčianska Skalka near Trenčín town (Lukáš 1987); 3 = upper Vistula valley, reserve 'Góry Pieprzowe' (BANASZAK 2003); 4 = lower Vistula valley. (The term 'southern' applies here to sub-Mediterranean, sub-Pontic, Ponto-Mediterranean species).

DISCUSSION

This work summarizes results of our research on wild bees of the xerothermic plant communities in the lower Vistula region. Some of the early results have already been published (BANASZAK 1975, 1980, BANASZAK, CIERZNIAK 1994), but the majority of data is original, collected in 1998–2002 with participation of also the remaining two authors. In total, 253 species of Apiformes were recorded at 17 studied sites (Appendix 1). It must be noted that at the current state of knowledge we could not distinguish reliably between females of *Halictus compressus* and *H. simplex*. In our earlier reports, the two species were jointly described as *H. tetrazonius* (see PESENKO ET AL. 2000). The recorded number of species is probably incomplete, because the studied, island-like sites are visited by bees from the neighbouring, different habitats. The true number of species in the study area probably reaches about 300 (estimated by the jackknife2 and chao2 methods). This number would be approximated to if we included the 38 species recorded by PAWLIKOWSKI AND HIRSCH (2002) in this region, but some of their records are doubtful. In particular, their determination of halictids was questioned by YU. A. PESENKO (PESENKO ET AL. 2000, p. 81). Of the records from the Vistula region listed by PAWLIKOWSKI and HIRSCH (2002), doubts are raised mainly by species like *Andrena similis* SMITH, *H. eurygnatus, Evylaeus intermedius* SCHENCK), *E. limbellus* (MORAWITZ), *E. nitidulus* (FABRICIUS) (= *H. aenaidorsus* ALFKEN), *Sphecodes croaticus* MEYER, *Osmia confusa* (MORAWITZ) and *Psithyrus norvegicus*.

The diversity of Apiformes in the study area (i.e. 253 recorded species and the estimated total of 300) must be regarded as very high, considering that our investigations involved nearly exclusively the xerothermic grasslands and thickets on the slopes of the lower Vistula valley. These numbers are comparable with numbers recorded in large regions of Poland, e.g. 270 in Pomerania, 320 in the Wielkopolska-Kujawy Lowland, and 270 in Małopolska (BANASZAK 1993). PESENKO (1971, 1975) in the steppes along the Don river recorded 347 species of Apiformes. In turn, OSYTSHNJUK (1959) in the steppes on the right side of the Dnieper river found 273 species, but if literature data from that part of the Ukraine are taken into account, then the total number of species in that area reaches 339. However, those numbers concern not only natural steppes but also bottomlands, dry ravines, forest islands, roadsides, and cultivated fields. The Moravian refuge is also rich in thermophilous species, as 213 species were found in Trenčianska Skalka (LUCAŠ 1987) and 146 in the nearby reserve Turecko (LUCAŠ 1983).

As mentioned in the Results, the Halictidae clearly dominated over bee families in our study area. Their large contribution is characteristic of open habitats, but particularly of xerothermic swards. This was observed also by PESENKO (1972 ab) in the steppes on the Don river, where in terms of diversity the Halictidae (74 species) dominated over other groups, also over the Andrenidae (54 species). In particular, *Lasioglossum bicallosum* (MORAWITZ) and *L. malachurum* were extremely abundant there. It is noteworthy that similarly high contributions of halictids were reported from lowlands in Romania (BANASZAK, MANOLE 1987) and the Polish Lowland (BANASZAK 1983).

The example of varied grasslands in the reserve 'Gruczno' shows how the soil and land relief affect plant communities and indirectly also the diversity of bee communities. The five plots of about 3 ha each differed greatly in total number of species (from 20 to nearly 80) and dominance structure. This allows us to conclude that in order to create a complete picture of the fauna, we should strive to maximize the number of sites and sampling sessions. This was also emphasized by NOSKIEWICZ (1934), while discussing the results of faunistic research in Podolye.

The species composition and structure of the studied xerothermic plant communities in the Vistula valley resemble those of the distant southeastern steppe communities dominated by *Stipa* spp. (CEYNOWA 1968). Thus it is not surprising that most of the 'southern' (Ponto-Mediterranean and Pontic) species recorded in our study area come from those refuges. Anyway, despite the floristic and faunistic similarity, the xerothermic grasslands along the Vistula are much poorer in 'southern' bee species than the Ukrainian steppes. This is due to the general northward decrease in diversity of xerothermophilous fauna. Besides, the Ukrainian steppes and grasslands in the Vistula valley differ in dynamics of bee emergence and abundance during the growing season, due to climatic differences (BANASZAK 1993). The Ukrainian steppe already in May reaches an optimum of its development but the plants finish their growth quickly because of long-term drought in summer. As a result, also bees are the most abundant in May and their numbers decrease dramatically in late July. By contrast, bee abundance in our study area increases to its optimum in July and starts to decline in mid-August (see Fig. 15 and BANASZAK 1993).

A short commentary must be added about the relatively small contribution of bumblebees, as they accounted for only 5% of the total catch. The value increases only slightly if we add cuckoo bees *Psythirus* spp. (Appendix 1). This reflects a general trend, as bumblebees are dominated by other groups of bees in xerothermic sites. They prefer colder and more humid habitats, as was proved earlier by BANASZAK (1996).

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APPENDIX 1.

List of species and numbers of individuals of Apiformes found at studied sites in the lower Vistula valley. Sources: A = BANASZAK (1980), B = BANASZAK, CIERZNIAK (1994), C = original data.† Column "Other sites" contains data from research sites studied only in 1970s: R = Raciążek near Toruń, C = Ciechocinek, O = Otłoczyn, L = Łęgnowo, K = Kiełp near Chełmno, S = Starogród, G = 'Gora św. Wawrzyńca'* number of trap-days (traps × days); + no quantitative data

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
No.	Investigation plot / Species	rez. "Kulin"		Bydgoszcz-Fordon	Strzelce Dolne	rez. "Kozielec"	Unisław	rez. "Zbocza Płutowskie"			rez. "Gruczno"		Świecie	Nowe n. Wisłą	rez. "Biała Góra"		other sites †	sum	percentage incidence
		Number of plots and period of investigation																	
		1		6	7	8	9	10			14		15	16	17		2-5, 11-13		
		A	C	C	C	C	C	A	B	C	A	C	C	C	A	C	A		
1	*Colletes cunicularius* (LINNAEUS, 1761)			2		5		2	1			20		3		9	Ł-2	44	0.4
2	*Colletes daviesanus* SMITH, 1846	23		2				22			1	11	1	37	9		G-2, R-3, Ł-3, S-2	116	1.2
3	*Colletes fodiens* (FOURCROY, 1785)			6				6			1	1	11	2	1	4	O-2, Ł-3	37	0.4
4	*Colletes marginatus* SMITH, 1846			5											3		K-1	9	0.1
5	*Colletes similis* SCHENCK, 1853		3	3								1		8				15	0.2
6	*Hylaeus angustatus* (SCHENCK, 1859)			1								1						2	< 0.1
7	*Hylaeus annularis* (KIRBY, 1802)	1	1	5				3	3		1	3	1	13	3		K-1, R-2	37	0.4
8	*Hylaeus bisinuatus* FÖRSTER, 1871					3												3	< 0.1
9	*Hylaeus brevicornis* NYLANDER, 1852		1	7		1						1		3				13	0.1

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
10	*Hylaeus communis* NYLANDER, 1852			4		2		1				1	1	2	5	14		30	0.3
11	*Hylaeus confusus* NYLANDER, 1852					1						3						4	< 0.1
12	*Hylaeus cornutus* CURTIS, 1831			3	1	1								5				10	0.1
13	*Hylaeus difformis* (EVERSMANN, 1852)															1		1	< 0.1
14	*Hylaeus gracilicornis* (MORAWITZ, 1867)					2		1				3			1		S-1	8	0.1
15	*Hylaeus gredleri* FÖRSTER, 1871			1		7							1					9	0.1
16	*Hylaeus hyalinatus* SMITH, 1842			2		4						1	1	2				10	0.1
17	*Hylaeus moricei* (FRIESE, 1898)					1						2						3	< 0.1
18	*Hylaeus nigritus* (FABRICIUS, 1798)												8	5	1	4		18	0.2
19	*Hylaeus punctatus* (BRULLÉ, 1832)												1					1	< 0.1
20	*Hylaeus sinuatus* (SCHENCK, 1853)			1		1								1				3	< 0.1
21	*Hylaeus styriacus* FÖRSTER, 1871		1			5												6	0.1
22	*Andrena alfkenella* PERKINS, 1914			7	1							6						14	0.1
23	*Andrena apicata* SMITH, 1847	1						3	1								Ł-1	6	0.1
24	*Andrena assimilis* RADOSZKOWSKI, 1876																C-4	4	< 0.1
25	*Andrena barbilabris* (KIRBY, 1802)	1					1				1	1						4	< 0.1
26	*Andrena bicolor* FABRICIUS, 1775					5							1	5			R-6, C-2	19	0.2
27	*Andrena bimaculata* (KIRBY, 1802)											1				1		2	< 0.1
28	*Andrena chrysosceles* (KIRBY, 1802)						1									2		3	< 0.1
29	*Andrena cineraria* (LINNAEUS, 1758)			2					1			1						4	< 0.1
30	*Andrena clarkella* (KIRBY, 1802)																Ł-1	1	< 0.1
31	*Andrena combinata* (CHRIST, 1791)			3		1	1	1	3			1						10	0.1
32	*Andrena curvungula* THOMSON, 1870					2		1					3					6	0.1
33	*Andrena decipiens* SCHENCK, 1859			1														1	< 0.1
34	*Andrena denticulata* (KIRBY, 1802)		3										1	3			C-1	8	0.1
35	*Andrena dorsata* (KIRBY, 1802)	3		6	1	2	1		2			7	2	8		3	C-1, Ł-3	41	0.4

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
36	*Andrena falsifica* PERKINS, 1915					4		11				13					Ł-1	29	0.3
37	*Andrena flavipes* PANZER, 1799	12		12	2	199		11	31		1	603	23	31		6	Ł-7	938	9.5
38	*Andrena floricola* EVERSMANN, 1852			1											1	1	R-1, C-3	7	0.1
39	*Andrena fucata* SMITH, 1847													1				1	< 0.1
40	*Andrena fulva* (MŰLLER, 1766)								1			18				2	Ł-2	23	0.2
41	*Andrena fulvago* ('(CHRIST, 1791)					1												1	< 0.1
42	*Andrena gelriae* van der VECHT, 1927		3	1				1			4	1		2				12	0.1
43	*Andrena gravida* IMHOFF, 1899			6	1	7		2	4			88	7	30		4		149	1.5
44	*Andrena haemorrhoa* (FABRICIUS, 1781)	4	1	8					2			27		8		11	Ł-6	67	0.7
45	*Andrena hattorfiana* (FABRICIUS, 1775)			1		1		17										19	0.2
46	*Andrena helvola* (LINNAEUS, 1758)	1				1		4	2			4					Ł-3	15	0.2
47	*Andrena jacobi* PERKINS, 1921					1		1	1			6				1	Ł-1	11	0.1
48	*Andrena labialis* (KIRBY, 1802)			1		1					4							6	0.1
49	*Andrena labiata* FABRICIUS, 1781					2						5				1		8	0.1
50	*Andrena lapponica* ZETTERSTEDT, 1838											3						3	< 0.1
51	*Andrena lepida* SCHENCK, 1859					1						5						6	0.1
52	*Andrena marginata* FABRICIUS, 1776	2																2	< 0.1
53	*Andrena minutula* (KIRBY, 1802)			6	2	1	1		7			44	6					67	0.7
54	*Andrena minutuloides* PERKINS, 1914	4	3	1	3	18	2	8				78	1	42		6	R-1, C-1	168	1.7
55	*Andrena mitis* SCHMIEDEKNECHT, 1883											13				2		15	0.2
56	*Andrena nanula* NYLANDER, 1848	1						2						2				5	0.1
57	*Andrena nasuta* GIRAUD, 1863										1							1	< 0.1
58	*Andrena nigriceps* (KIRBY, 1802)			1							1							2	< 0.1
59	*Andrena nigroaenea* (KIRBY, 1802)							2	1			13	1					17	0.2
60	*Andrena nitida* (MŰLLER, 1776)	2				4		6	10			32		5		2	Ł-1	62	0.6
61	*Andrena niveata* FRIESE, 1887											1						1	< 0.1

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
62	*Andrena nycthemera* IMHOFF, 1866											1						1	< 0.1
63	*Andrena ovatula* (KIRBY, 1802)			14	1		2	5				2	1	2				27	0.3
64	*Andrena paucisquama* NOSKIEWICZ, 1924					2		2										4	< 0.1
65	*Andrena pilipes* NOSKIEWICZ, 1924			1				2			1	1		3			Ł-1	9	0.1
66	*Andrena praecox* (SCOPOLI, 1763)											32		1				33	0.3
67	*Andrena proxima* (KIRBY, 1802)					3	2									4		9	0.1
68	*Andrena rosae* PANZER, 1801	1		1		1		14			1	3	1	47	2			71	0.7
69	*Andrena schencki* MORAWITZ, 1866			1				1										2	< 0.1
70	*Andrena subopaca* NYLANDER, 1848		2	1		2						40		3		6		54	0.5
71	*Andrena suerinensis* FRIESE, 1884										1							1	< 0.1
72	*Andrena symphyti* SCHMIEDEKNECHT, 1883	1						1										2	< 0.1
73	*Andrena synadelpha* PERKINS, 1914								3			1						4	< 0.1
74	*Andrena tibialis* (KIRBY, 1802)	2		5			2					3	1	3				16	0.2
75	*Andrena vaga* PANZER, 1799					10		4	5			468	13	3		12	Ł-4	519	5.2
76	*Andrena varians* (ROSSI, 1781)	1		1				2				1					Ł-2	7	0.1
77	*Andrena ventralis* IMHOFF, 1832	3		1		2		20	3			29	3	4				65	0.7
78	*Panurgus calcaratus* (SCOPOLI, 1763)							1					2	1			G-1, Ł-1	6	0.1
79	*Dufouera inermis* (NYLANDER, 1848)											1						1	< 0.1
80	*Nomioides minutissimus* (ROSSI, 1790)																O-3	3	< 0.1
81	*Halictus simplex* BLŰTHGEN, 1923							2	2		1	1	2				K-5, G-1	14	0.2
81	*Halictus compressus*/simplex	6	2			7		12	1		7	86	3	1			R-2, S-2	129	1.3
82	*Halictus maculatus* SMITH, 1848		3	2		109		1	4			10	41	17			K-1, Ł-4	192	1.9
83	*Halictus quadricinctus* (FABRICIUS, 1776)			1	1	14		8			5	10		18			C-1, S-5	63	0.7
84	*Halictus rubicundus* (CHRIST, 1791)			4		6		7			2	27		1	1		K-1, C-1	50	0.5
85	*Halictus sexcinctus* (FABRICIUS, 1775)	1		7		2		3			2	3	1	4		1	O-3, G-3, K-1, Ł-5, S-3	39	0.4

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
86	*Seladonia confusa* (SMITH, 1853)			5				2				3	2		2	2	O-2	18	0.2
87	*Seladonia leucahenea* (EBMER, 1972)		1	9		2									1		Ł-1	14	0.2
88	*Seladonia subaurata* (ROSSI, 1792)	2	3	3		16		19	1		1	173	82	11			O-11, G-1, K-4, S-1	328	3.3
89	*Seladonia tumulorum* (LINNAEUS, 1758)	3	4	11	2	13		22	13		1	138	119	9		2	O-1, R-1, S-2	341	3.4
90	*Lasioglossum costulatum* (KRIECHBAUMER, 1873)							1			1	1						3	< 0.1
91	*Lasioglossum laevigatum* (Kirby, 1802)			3	1	2	3	13	6			5		1				34	0.3
92	*Lasioglossum lativentre* (SCHENCK, 1853)							2			2							4	< 0.1
93	*Lasioglossum leucozonium* (SCHRANK 1792)	1		3			2				1	6		2			R-1, S-1	17	0.2
94	*Lasioglossum majus* (NYLANDER, 1852)	1	1	1	1							3	1					8	0.1
95	*Lasioglossum quadrinotatum* (SMITH, 1848)					2		3			1	15					C-1	22	0.2
96	*Lasioglossum sexnotatum* (KIRBY, 1802)	1		3				3	1	1	2	4	4					19	0.2
97	*Lasioglossum xanthopus* (KIRBY, 1802)			1		4		3				1	1					10	0.1
98	*Lasioglossum zonulum* (SMITH, 1848)							1					1					2	0
99	*Evylaeus aeratus* (KIRBY, 1802)			1		1						15				1		18	0.2
100	*Evylaeus albipes* (FABRICIUS, 1781)		1	2								2					K-1	7	0.1
101	*Evylaeus calceatus* (SCOPOLI, 1763)	4		8	3	7		11	1			63	1	8	2	6	G-1, R-6, C-2, Ł-7	130	1.3
102	*Evylaeus convexiusculus* (SCHENCK, 1853)					1						14	3					18	0.2
103	*Evylaeus fulvicornis* (KIRBY, 1802)	3	1			2		41	33	1	2	163	5	7	1		G-1, R-1, Ł-1	262	2.6
104	*Evylaeus interruptus* (PANZER, 1798)							1										1	< 0.1
105	*Evylaeus laevis* (KIRBY, 1802)							4			2						G-1	7	0.1
106	*Evylaeus laticeps* (SCHENCK, 1868)	2				7		14	6		1	223	12	6		1	O-1, Ł-5	278	2.8
107	*Evylaeus leucopus* (KIRBY, 1802)			1								1						2	< 0.1
108	*Evylaeus linearis* (SCHENCK, 1868)			1		2		1				582	6					592	6.0
109	*Evylaeus lucidulus* (SCHENCK, 1861)			2		1						9	1	1				14	0.2
110	*Evylaeus malachurus* (KIRBY, 1802)		4									1						5	0.1
111	*Evylaeus minutissimus* (KIRBY, 1802)											10		1				11	0.1

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
112	*Evylaeus morio* (FABRICIUS, 1793)	9	7	2	2	18	1	26	39			1037	254	11	1	2	Ł-6, S-2	1417	14.3
113	*Evylaeus nigripes* (LEPELETIER, 1841)							1										1	< 0.1
114	*Evylaeus nitidiusculus* (Kirby, 1802)					1		1										2	< 0.1
115	*Evylaeus parvulus* (SCHENCK, 1853)			4		2			10			4	2					22	0.2
116	*Evylaeus pauxillus* (SCHENCK, 1853)	6		17	2	28		8	95			455	13	21		2	G-1, Ł-3, S-1	652	6.6
117	*Evylaeus politus* (SCHENCK, 1853)		3															3	< 0.1
118	*Evylaeus punctatissimus* (SCHENCK, 1853)							1				3						4	< 0.1
119	*Evylaeus quadrinotatulus* (SCHENCK, 1861)							2					2					4	< 0.1
120	*Evylaeus rufitarsis* (ZETTERSTEDT, 1838)											12						12	0.1
121	*Evylaeus sabulosus* (WARNCKE, 1986)			1								4				1		6	0.1
122	*Evylaeus semilucens* (ALFKEN, 1914)											4		1				5	0.1
123	*Evylaeus sexstrigatus* (SCHENCK, 1868)		1	6														7	0.1
124	*Evylaeus tarsatus* (SCHENCK, 1868)											12						12	0.1
125	*Evylaeus villosulus* (KIRBY, 1802)			4			5					4	2	1				16	0.2
126	*Rhophitoides canus* (EVERSMANN, 1852)	1		1	1				3					5			S-1	12	0.1
127	*Rophites algirus* PÉREZ, 1895					12												12	0.1
128	*Rophites quinquespinosus* SPINOLA, 1808		1							2		1	1				R-1	6	0.1
129	*Sphecodes albilabris* (FABRICIUS, 1793)			1		3	1	7	2			3	3	5	2	16		43	0.4
130	*Sphecodes crassus* THOMSON, 1870		2	1		12		1				12	18	4			Ł-1	51	0.5
131	*Sphecodes ephippius* (LINNAEUS, 1767)		2			8		1	13		1	29		5		9		68	0.7
132	*Sphecodes ferruginatus* HAGENS, 1882					3		2	1			37						43	0.4
133	*Sphecodes geofrellus* (KIRBY, 1802)			1		3						1						5	0.1
134	*Sphecodes gibbus* (LINNAEUS, 1758)					11	1	1				3	10	1		2		29	0.3
135	*Sphecodes hyalinatus* HAGENS, 1882					2		12	1			9	1					25	0.3
136	*Sphecodes longulus* HAGENS, 1882											2						2	< 0.1
137	*Sphecodes marginatus* HAGENS, 1882			1								4	2					7	0.1

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
138	*Sphecodes miniatus* HAGENS, 1882												3					3	< 0.1
139	*Sphecodes monilicornis* (KIRBY, 1802)	1		1		51		2				35	6			6	C-1	103	1.0
140	*Sphecodes niger* HAGENS, 1882		1					1				2	33					37	0.4
141	*Sphecodes pellucidus* SMITH, 1845			3		7		3				6	15	5		2	C-1	42	0.4
142	*Sphecodes puncticeps* THOMSON, 1870								1			1						2	< 0.1
143	*Sphecodes reticulatus* THOMSON, 1870											1					Ł-1	2	< 0.1
144	*Sphecodes ruficrus* (ERICHSON, 1835)								1									1	< 0.1
145	*Sphecodes rufiventris* (PANZER, 1798)					1						3		2				6	0.1
146	*Sphecodes spinulosus* HAGENS, 1875								1									1	< 0.1
147	*Melitta leporina* (PANZER, 1799)	6		10	3	1		1			2	2	1	6	6		C-2, Ł-1, S-2	43	0.4
148	*Melitta nigricans* ALFKEN, 1905		1	7	3							3	1					15	0.2
149	*Melitta tricincta* KIRBY, 1802							2									S-2	4	< 0.1
150	*Macropis fulvipes* (FABRICIUS, 1804)												1					1	< 0.1
151	*Macropis europaea* WARNCKE, 1973												1					1	< 0.1
152	*Dasypoda altercator* (HARRIS, 1776)	2	1	16	1	1		7			2	11	1	6	5		O-2, G-2, K-1, R-2, C-1	61	0.6
153	*Anthidium manicatum* (LINNAEUS, 1758)			1		1								8			Ł-2, S-8	20	0.2
154	*Anthidium punctatum* LATREILLE, 1809														1			1	< 0.1
155	*Proanthidium oblongatum* LATREILLE, 1809			1								1	1					3	< 0.1
156	*Anthidiellum strigatum* (PANZER, 1805)					1									2	1		4	< 0.1
157	*Stelis punctulatissima* (KIRBY, 1802)			1		3												4	< 0.1
158	*Heriades crenulatus* NYLANDER, 1856			1								2				10	O-3	16	0.2
159	*Heriades truncorum* (LINNAEUS, 1758)			1		1						1		1		1	G-1	6	0.1
160	*Chelostoma campanularum* (Kirby, 1802)											7					R-2, Ł-11, S-3	13	0.2
161	*Chelostoma rapunculi* (Lepeletier, 1841)			2		1	1						3	1			C-1, S-1	10	0.1
162	*Anthocopa bidentata* (Morawitz, 1876)	1															S-1	2	< 0.1

1	**2**	**3**		**4**	**5**	**6**	**7**	**8**			**9**		**10**	**11**	**12**		**13**	**14**	**15**
163	*Anthocopa papaveris* (Latreille, 1799)			1							1	9					K-1	12	0.1
164	*Anthocopa spinulosa* (Kirby, 1802)					7								9			S-2	18	0.2
165	*Hoplitis adunca* (Panzer, 1798)		6	2		6			1		1	7			1			24	0.2
166	*Hoplitis anthocopoides* (Schenck, 1853)		1	2		7						1		1			Ł-3	15	0.2
167	*Hoplitis leucomelana* (Kirby, 1802)		1	1		1			2							2		7	0.1
168	*Hoplitis tridentata* (Dufour et Perris 1840)			1														1	< 0.1
169	*Osmia aurulenta* (Panzer, 1799)													1				1	< 0.1
170	*Osmia brevicornis* (Fabricius, 1798)			1														1	< 0.1
171	*Osmia coerulescens* (Linnaeus, 1758)		1			2						2		1				6	0.1
172	*Osmia leaiana* (Kirby, 1802)							1									S-1	2	< 0.1
173	*Osmia mustelina* Gerstaecker, 1869										1							1	< 0.1
174	*Osmia rufa* (Linnaeus, 1758)	1		1		6						5		1		3	Ł-1	18	0.2
175	*Chalicodoma ericetorum* (Lepeletier, 1841)													1				1	< 0.1
176	*Megachile alpicola* Alfken, 1924			1										1				2	< 0.1
177	*Megachile apicalis* Spinola, 1808							1										1	< 0.1
178	*Megachile argentata* (Fabricius, 1793)			1														1	< 0.1
179	*Megachile centuncularis* (Linnaeus, 1758)	1										3	1					5	0.1
180	*Megachile circumcincta* (Kirby, 1802)			3				1	1			4	1	4				14	0.2
181	*Megachile lagopoda* (Linnaeus, 1761)							2									S-1	3	< 0.1
182	*Megachile leachella* Curtis, 1828												1		3		Ł-2	6	0.1
183	*Megachile ligniseca* (Kirby, 1802)					2				1				1				4	< 0.1
184	*Megachile maritima* (Kirby, 1802)			3														3	< 0.1
185	*Megachile pilidens* Alfken, 1923	2				2					3					1	S-2	10	0.1
186	*Megachile rotundata* (Fabricius, 1784)															1	O-2	3	< 0.1
187	*Megachile versicolor* Smith, 1844		1	4		2							2	2				11	0.1
188	*Megachile willughbiella* (Kirby, 1802)			3														3	< 0.1

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
189	*Coelioxys brevis* EVERSMANN, 1852														1			1	< 0.1
190	*Coelioxys conoidea* (ILLIGER, 1806)			6		1					1				1			9	0.1
191	*Coelioxys elongata* LEPELETIER, 1841			1														1	< 0.1
192	*Coelioxys inermis* (KIRBY, 1802)											1						1	< 0.1
193	*Coelioxys mandibularis* Nylander, 1848					3						6						9	0.1
194	*Coelioxys quadridentata* (Linnaeus, 1758)		1	1								1	2	1		2		8	0.1
195	*Coelioxys rufescens* LEPELETIER, 1825					1							2	2				5	0.1
196	*Anthophora bimaculata* (PANZER, 1798)			18				7					1		14		O-2, G-4, Ł-3	49	0.5
197	*Anthophora furcata* (PANZER, 1798)																R-1	1	< 0.1
198	*Anthophora plumipes* (PALLAS, 1772)	4				2		7				4	4	4		13	Ł-3	41	0.4
199	*Anthophora pubescens* (Fabricius, 1781)	1															R-2	3	< 0.1
200	*Anthophora retusa* (LINNAEUS, 1758)	3		1				5			1							10	0.1
201	*Melecta punctata* (FABRICIUS, 1775)	1				7			1				1			2		12	0.1
202	*Eucera interrupta* BAER, 1850										8							8	0.1
203	*Eucera longicornis* (LINNAEUS, 1758)			1			5	12				2						20	0.2
204	*Tetralonia dentata* (KLUG, 1835)			2														2	< 0.1
205	*Tetralonia macroglossa* ILLIGER, 1806					2						17					R-6	25	0.3
206	*Ceratina cyanea* (KIRBY, 1802)			2				2	2		1	10		1	1	3	K-1, R-1, Ł-1	25	0.3
207	*Nomada bifasciata* OLIVIER, 1811											2						2	< 0.1
208	*Nomada fabriciana* (LINNAEUS, 1767)													1		1		2	< 0.1
209	*Nomada flava* PANZER, 1798							1										1	< 0.1
210	*Nomada flavoguttata* (KIRBY, 1802)		1	1				5	1			7		4		1	C-2, Ł-1	23	0.2
211	*Nomada flavopicta* (KIRBY, 1802)							4			2	1	1	1			O-1, Ł-1, K-2, C-5	18	0.2
212	*Nomada fucata* PANZER, 1798	8		1		84		3	7			22	17	15		1	Ł-1	159	1.6
213	*Nomada furva* PANZER, 1798											1						1	< 0.1
214	*Nomada fuscicornis* NYLANDER, 1848							4										4	< 0.1

1	**2**	**3**		**4**	**5**	**6**	**7**	**8**			**9**		**10**	**11**	**12**		**13**	**14**	**15**
215	*Nomada goodeniana* (KIRBY, 1802)	2				1		1	1			1	1	4		2		13	0.1
216	*Nomada guttulata* SCHENCK, 1861											1						1	< 0.1
217	*Nomada lathburiana* (KIRBY, 1802)	2				3		5	7			13	9	9		26	Ł-3	77	0.8
218	*Nomada leucophthalma* (KIRBY, 1802)							1				3		1		1		6	0.1
219	*Nomada lineola* (KIRBY, 1802)			1														1	< 0.1
220	*Nomada marshamella* (KIRBY, 1802)	1	1	5					3					4				14	0.2
221	*Nomada moeschleri* ALFKEN, 1913	1	2					4				12		4		2		25	0.3
222	*Nomada ochrostoma* (Zetterstedt, 1838)							43	1		2	5	2	2				55	0.6
223	*Nomada panzeri* LEPELETIER, 1841					1		1				1		1		5		9	0.1
224	*Nomada roberjeotiana* PANZER, 1799							1			4						G-4, K-1, R-1, Ł-1, S-1	13	0.1
225	*Nomada ruficornis* (LINNAEUS, 1758)	1		1				2				4	1			1		10	0.1
226	*Nomada rufipes* FABRICIUS, 1793										1							1	< 0.1
227	*Nomada sheppardana* (KIRBY, 1802)												3					3	< 0.1
228	*Nomada signata* JURINE, 1807								1			3				1		5	0.1
229	*Nomada striata* FABRICIUS, 1793								1									1	< 0.1
230	*Nomada zonata* PANZER, 1798												1					1	< 0.1
231	*Epeolus variegatus* (LINNAEUS, 1758)	1		3		1		2				1	5	1	6	1	G-2, K-1, C-2, Ł-1, S-1	28	0.3
232	*Bombus hortorum* (LINNAEUS, 1761)					1	1	3	1		3	3	2	2	1	1	R-2, C-5	25	0.3
233	*Bombus humilis* ILLIGER, 1806							2			4				8		Ł-4	18	0.2
234	*Bombus hypnorum* (LINNAEUS, 1758)	1					1				1				1	1	C-2, Ł-2	9	0.1
235	*Bombus jonellus* (KIRBY, 1802)											1						1	< 0.1
236	*Bombus lapidarius* (LINNAEUS, 1758)	1	1	5		13		4	18		3	11	5	37	4	2	O-1, R-1, C-4, Ł-2	112	1.1
237	*Bombus lucorum* (LINNAEUS, 1761)	1		12					5		2	15		9	2	4	Ł-2	52	0.5
238	*Bombus muscorum* (LINNAEUS, 1758)										1	1			3		C-4	9	0.1
239	*Bombus pascuorum* (SCOPOLI, 1763)	1	4	13	1	4	1	1				6	12	13	1	11	C-1, Ł-3	72	0.7

1	2	3		4	5	6	7	8			9		10	11	12		13	14	15
240	*Bombus pratorum* (LINNAEUS, 1761)		5	1		3	1					1		1				12	0.1
241	*Bombus ruderarius* (MÜLLER, 1776)					5		2	2			3			2	3	C-5, Ł-4	26	0.3
242	*Bombus ruderatus* (FABRICIUS, 1775)			1														1	< 0.1
243	*Bombus semenoviellus* SKORIKOV, 1910			1		5								1				7	0.1
244	*Bombus subterraneus* (LINNAEUS, 1758)							1			1							2	< 0.1
245	*Bombus sylvarum* (LINNAEUS, 1761)	1		10	1	17	2	3			2	4	1	4	2	3	K-1, C-4, Ł-3, S-1	59	0.6
246	*Bombus terrestris* LINNAEUS, 1758	1	3	2		1			6			18	4	18	2	14	O-1, C-2, Ł-1	73	0.7
247	*Bombus veteranus* (FABRICIUS, 1793)					1											Ł-1	2	< 0.1
248	*Psithyrus bohemicus* (SEIDL, 1837)			1		1			2			1	1	2	2	12	O-3, S-1	26	0.3
249	*Psithyrus campestris* (PANZER, 1801)					1				3							S-1	5	0.1
250	*Psithyrus rupestris* (FABRICIUS, 1793)										1	1		2				4	< 0.1
251	*Psithyrus sylvestris* LEPELETIER, 1832		1															1	< 0.1
252	*Psithyrus vestalis* (GEOFFROY in FOURCROY, 1785)					1		2			2						O-2, C-1	8	0.1
253	*Apis mellifera* LINNAEUS, 1758	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		-	-
Number of individuals		148	86	389	34	867	38	543	379	8	100	5095	830	621	105	281	366	9896	100.0
Number of species		54	42	114	21	108	22	101	59	5	52	148	87	98	38	67	95	255	
		81						125			165				85				
Number of samples		3	2	54	2	23	2	8	11	1	3	16 1666*	18	10 315*	2	5 282*	10	173 2263*	

APPENDIX 2

Comparison of diversity of 'southern' species of Apiformes in the Podolye refuge (Dniester valley) and in the valley of upper Vistula ('Góry Pieprzowe') and lower Vistula, based on original and published data.

Podolye	Upper Vistula	Lower Vistula
	Colletidae	
Hylaeus styriacus FÖRST.	*Hylaeus styriacus* FÖRST.	*Hylaeus styriacus* FÖRST.
Colletes punctatus MOCS.	*Colletes punctatus* MOCS.	-
Colletes inexpectatus NOSK.	*Colletes inexpectatus* NOSK.	-
Hylaeus variegatus (F.)	*Hylaeus variegatus* (F.)	-
Hylaeus cornutus Curt.	-	*Hylaeus cornutus* CURT.
Hylaeus difformis (EV.)	-	*Hylaeus difformis* (EV.)
Colletes anchusae NOSK.	-	-
Colletes eous Morice	-	-
Colletes hylaeiformis EV.	-	-
Colletes nasutus SM.	-	-
-	-	*Hylaeus punctatus* (BRULLÉ)
	Andrenidae	
Andrena curvungula THOMS.	*Andrena curvungula* THOMS.	*Andrena curvungula* THOMS.
Andrena flavipes PZ..	*Andrena flavipes* PZ.	*Andrena flavipes* PZ.
Andrena gerliae VECHT	*Andrena gelriae* VECHT	*Andrena gelriae* VECHT
Andrena paucisquama NOSK.	*Andrena paucisquama* NOSK.	*Andrena paucisquama* NOSK.
Andrena chrysopyga SCHCK.	*Andrena chrysopyga* SCHCK.	-
Andrena combinata CHR..	*Andrena combinata* (CHR.)	-
Andrena marginata F.	-	*Andrena marginata* F.
Andrena nasuta GIR.	-	*Andrena nasuta* Giraud
Andrena truncatilabris MOR.	-	-
Andrena aeneiventris MOR.	-	-
Andrena albopunctata ROSSI	-	-
Andrena atrata FRIESE	-	-

Andrena bucephala STEPH.	-	-
Andrena chrysopus PÈR.	-	-
Andrena hypopolia PÈR.	-	-
Andrena incisa EV.	-	-
Andrena limata SM.	-	-
Andrena nanaeformis MOR.	-	-
Andrena nuptialis PÈR.	-	-
Andrena pandellei SAUND.	-	-
Andrena pilipes F.	-	-
Andrena polita SM..	-	-
Andrena potentillae PZ.	-	-
Andrena sericata IMH.	-	-
Andrena succincta F.	-	-
Andrena taraxaci GIR.	-	-
Andrena tenuis MOR.	-	-
Camptopoeum frontale F.	-	-
Melitturga clavicornis LATR.	-	-
Panurginus labiatus EV.	-	-
Panurginus sculpturatus MOR.	-	-
-	*Andrena assimilis* RAD.	-
-	*Andrena susterai* ALFK.	-
-	-	*Andrena decipiens* SCHCK.
-	-	*Andrena lepida* SCHCK.
-	-	*Andrena niveata* FRIESE
-	-	*Andrena suerinensis* FRIESE
	Melittidae	
Dasypoda argentata PANZ.	-	-
Melitta budensis MOCS.	-	-
Melitta dimidiata MOR.	-	-
	Halictidae	
Rophites quinquesinosus SPIN.	*Rophites quinquespinosus* SPIN.	*Rophites quinquespinosus* SPIN.
Rhophitoides canus (EV.)	*Rhophitoides canus* (EV.)	*Rhophitoides canus* (EV.)

Halictus simplex BL.	*Halictus compressus* (WALCK.)	*Halictus compressus*/simplex
Seladonia subaurata (ROSSI)	*Seladonia subaurata* (ROSSI)	*Seladonia subaurata* (ROSSI)
Evylaeus convexiusculus (SCHCK.)	*Evylaeus convexiusculus* (SCHCK.)	*Evylaeus convexiusculus* (SCHCK.)
Evylaeus nigripes (LEP.)	*Evylaeus nigripes* (LEP.)	*Evylaeus nigripes* (LEP.)
Evylaeus pauxillus (SCHCK)	*Evylaeus pauxillus* (SCHCK.)	*Evylaeus pauxillus* (SCHCK.)
Rhophites hartmanni FRIESE	*Rophites hartmanni* FRIESE	-
Evylaeus glabriusculus (MOR.)	*Evylaeus glabriusculus* (MOR.)	-
Evylaeus interruptus (PZ.)	*Evylaeus interrupus* (PZ.)	-
Evylaeus limbellus (MOR.)	*Evylaeus limbellus* (MOR.)	-
Evylaeus minutulus (SCHCK.)	*Evylaeus minutulus* (SCHCK.)	-
Evylaeus politus (SCHCK.)	*Evylaeus politus* (SCHCK.)	-
Evylaeus setulellus (STRAND)	*Evylaeus setulellus* (STRAND)	-
Evylaeus tricinctus (SCHCK.)	*Evylaeus tricinctus* (SCHCK.)	-
Evylaeus marginellus SCHCK.	*Evylaeus marginellus* (SCHCK.)	-
Evylaeus quadrisignatus (SCHCK.)	-	*Sphecodes rufiventris* (PZ.)
Sphecodes rufiventris (PZ.)	-	*Sphecodes rufiventris* (PZ.)
Systropha planidens GIR.	-	-
Halictus sexcinctus (F.)	-	-
Seladonia kessleri (Brahms.)	-	-
Lasioglossum discum (SM.)	-	-
Lasioglossum pallens (BRULLÈ)	-	-
Lasioglossum prasinum (SM.)	-	-
Lasioglossum subfasciatum (IMH.)	-	-
Evylaeus clypearis (SCHCK.)	-	-
Evylaeus buccalis (PÈR.)	-	-
Evylaeus corvinus (MOR.)	-	-
Evylaeus duckei (ALFK.)	-	-
Evylaeus elegans (LEP.)	-	-
Evylaeus marginatus (BRULLÈ)	-	-
Evylaeus podolicus (NOSK.)	-	-
Evylaeus puncticolis (MOR.)	-	-
Evylaeus pygmaeus (SCHCK.)	-	-

Evylaeus trichopygus (BL.)	-	-
Evylaeus truncaticollis (MOR.)	-	-
Sphecodes croaticus MEYER	-	-
Sphecodes marginatus HAG.	-	-
Sphecodes schencki HAG.	-	-
-	*Lasioglossum lativentre* (SCHCK.)	*Lasioglossum lativentre* (SCHCK.)
-	*Evylaeus linearis* (SCHCK.)	*Evylaeus linearis* (SCHCK.)
-	*Evylaeus malachurus* (KBY.)	*Evylaeus malachurus* (KBY.)
-	*Evylaeus tarsatus* (SCHCK.)	*Evylaeus tarsatus* (SCHCK.)
-	*Sphecodes ferruginatus* HAG.	*Sphecodes ferruginatus* HAG.
-	*Evylaeus obscuratus* (MOR.)	-
-	*Sphecodes cristatus* HAG.	-
-	-	*Lasioglossum majus* (NYL.)
-	-	*Sphecodes niger* HAG.
	Megachilidae	
Proanthidium oblongatum LATR.	*Proanthidium oblongatum* LATR.	*Proanthidium oblongatum* LATR.
Heriades crenulatus NYL.	*Heriades crenulatus* NYL.	*Heriades crenulatus* NYL.
Anthocopa papaveris (LATR.)	*Anthocopa papaveris* (LATR.)	*Anthocopa papaveris* (LATR.)
Osmia brevicornis (F.)	*Osmia brevicornis* (F.)	*Osmia brevicornis* (F.)
Megachile pilidens ALFK.	*Megachile pilidens* ALFK.	*Megachile pilidens* ALFK.
Chelostoma distinctum STÖCKH.	*Chelostoma distinctum* Stoeckh.	-
Paranthidiellum lituratum PZ.	*Paraanthidiellum lituratum* (PZ.)	-
Anthocopa tergestensis (DUCKE)	*Anthocopa tergestensis* (DUCKE)	-
Osmia cerinthidis MOR.	*Osmia cerinthidis* MOR.	-
Hoplitis tridentata (DUF. et PER.)	-	*Hoplitis tridentata* (DUF. et PER.)
Anthocopa bidentata (MOR.)	-	*Anthocopa bidentata* (MOR.)
Anthocopa spinulosa (KBY.)	-	*Anthocopa spinulosa* (KBY.)
Osmia aurulenta (PZ.)	-	*Osmia aurulenta* (PZ.)
Trachusa byssina (PZ.)	-	-
Anthidium cingulatum LATR.	-	-
Anthidium florentinum(F.).	-	-
Anthidium interruptum F.	-	-

Dioxys cincta JUR.	-	-
Stelis odontopyga NOSK.	-	-
Stelis phaeoptera (KBY.)	-	-
Stelis simillima MOR.	-	-
Hoplitis manicata MORICE	-	-
*Hoplitis praestans (*MOR.)	-	-
*Hoplitis rufohirta (*LATR.)	-	-
Anthocopa andrenoides (SPIN.)	-	-
Anthocopa mocsaryi (FRIESE)	-	-
Chalicodoma hungarica MOCS.	-	-
Osmia cornuta (LATR.)	-	-
Megachile apicalis SPIN.	-	-
Megachile argentata (F.)	-	-
Megachile dorsalis PÈR.	-	-
Megachile giraudi GERST.	-	-
Megachile pilicrus MOR.	-	-
Megachile rubrimana MOR.	-	-
Coelioxys haemorrhoa FÖRST.	-	-
Coelioxys obtusa PÈR.	-	-
-	-	*Osmia mustelina* GERST.
-	-	*Megachile rotundata* (F.)
-	-	*Coelioxys brevis* EV.
	Anthophoridae	
*Anthophora pubescens (*F.)	*Anthophora pubescens* (F.)	*Anthophora pubescens* (F.)
Eucera interrupta BAER	*Eucera interrupta* BAER	*Eucera interrupta* BAER
Anthophora plagiata (ILL.)	*Anthophora plagiata* (ILL.)	-
*Melecta luctuosa (*SCOP.)	*Melecta luctuosa* (SCOP.)	-
Biastes brevicornis (PZ.)	*Biastes brevicornis* (PZ.)	-
Tetralonia h. hungarica (FRIESE)	*Tetralonia hungarica* (FRIESE)	-
Nomada nobilis H.-SCH.	*Nomada nobilis* H.-SCH.	-
Tetralonia dentata (KLUG)	-	*Tetralonia dentata* (KLUG)
Tetralonia macroglossa ILL.	-	*Tetralonia macroglossa* ILL.

Anthophora astragali MOR.	-	-
Anthophora crinipes SM.	-	-
Anthophora pubescens (F.)	-	-
Anthophora quadrimaculata (PZ.)	-	-
Amegilla albigena LEP.	-	-
Amegilla quadrifasciata (VILL.)	-	-
Amegilla salviae (MOR.)	-	-
Thyreus orbatus LEP.	-	-
Eucera clypeata ERICH.	-	-
Eucera nigrifacies LEP.	-	-
Eucera taurica MOR.	-	-
Tetralonia nana Mor.	-	-
Tetralonia ruficornis (F.)	-	-
Tetralonia scabiosae MOSC.	-	-
Tetralonia spectabilis MOR.	-	-
Xylocopa valga GERST.	-	-
Xylocopa violacea SCOP.	-	-
Nomada atroscutellaris STR.	-	-
Nomada basalis H.-SCH.	-	-
Nomada castellana DUSMET	-	-
Nomada emarginata MOR.	-	-
Nomada errans LEP.	-	-
Nomada femoralis MOR.	-	-
Nomada kohli SCHMIEDKN.	-	-
Nomada trispinosa SCHMIEDKN	-	-
Pasites maculatus JUR.	-	-
Parammobatodes minutus (Mocsary)	-	-
Ammobates vinctus GERST.	-	-
Ammobatoides abdominalis (EV.)	-	-
Biastes emarginatus (SCHCK.)	-	-
Biastes truncatus NYL.	-	-
Epeolus schummeli SCHILL.	-	-

-	-	-
-	-	-
-	-	-
-	-	*Nomada bifasciata* OLIV.
-	-	*Nomada furva* PZ.
-	-	*Nomada sheardana* (KBY.)
-	-	*Nomada zonata* PZ.
	Apidae	
Bombus cullumanus serrisquama (MOR.)	-	-
Bombus fragrans (PALL.)	-	-
Bombus argillaceus SCOP.	-	-
Bombus armeniacus RAD.	-	-
Psithyrus maxillosus KLUG	-	-