Biogeographical links between steppe insects in the Monegros region (Aragón, NE Spain), the eastern Mediterranean, and central Asia

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Abstract. Sixty-two species of insects in thirty-six families and nine orders, plus one species of Acari, were found to have disjunct distributions, or to belong to species groups with disjunct distributions, between the steppe areas in the central Monegros region (NE Spain) and the steppes in the eastern Mediterranean or central Asia. The accumulation of examples of a wide range of taxonomic groups, and the phyletic links of apparent endemic species of the central Ebro valley with eastern species, are considered to support the pre-Pleistocene origin of their relict distributions, associated with the persistence of steppe habitats over gypsiferous soils in the area since the Late Tertiary. The case of disjunct distributions of phytophages and their parasitoids on plants with disjunct distributions themselves, such as *Krascheninnikovia ceratoides* (L.) Gueldenst. (Chenopodiaceae) or the *Juniperus thurifera* L. − *J. excelsa* Bieb. complex (Cupressaceae), would seem to provide strong evidence supporting the continuity of their presence in the central Ebro valley through the Quaternary.

Key words. Ebro valley, insects, disjunct distributions, biogeography, gypsiferous soils, steppe habitats.

Resumen. Se relacionan 62 especies de insectos pertenecientes a 36 familias y 9 órdenes, más una especie de ácaro, con distribuciones dis juntas, o que pertenencen a grupos de especies con distribuciones dis juntas, entre las estepas de la región de los Monegros (NE de España) y las estepas del este mediterráneo y de Asia central. La acumulación de ejemplos de distintos grupos taxonómicos, y las relaciones filéticas de las especies aparentemente endémicas del valle medio del Ebro con especies orientales, apoyan la hipótesis del origen prepleistocénico de sus distribuciones relictas, asociadas con la persistencia de hábitats esteparios sobre suelos yesosos en la zona desde fines del Terciario. El caso de las distribuciones disjuntas de fitófagos y sus parasitoides sobre plantas también con distribuciones dis juntas, como *Krascheninnikovia ceratoides* (L.) Gueldenst. (Chenopodiaceae) o el complejo *Juniperus thurifera* L. − *J. excelsa* Bieb. (Cupressaceae), supone una evidencia adicional en favor de su continuidad en el valle medio del Ebro durante el Cuaternario.

Palabras clave. Valle del Ebro, insectos, distribuciones disjuntas, biogeografía, yesos, habitats esteparios.

INTRODUCTION

The disjunct distribution of taxa between the west and east Mediterranean, and, on a larger scale, between the western Mediterranean and central Asia, has traditionally been a major theme in south European biogeography (see, e.g. Brehm, 1947 for a detailed list of examples of Iberian and Balkanic plants, the so called Kiermack disjunction, or Banarescu, 1991 for examples among the Mediterranean fresh-water fauna). The pre-Pleistocene origin of at least some of the disjunct distributions of plants is now generally accepted (e.g. Braun-Blanquet & Bolòs *et al.*, 1957; Davis & Hedge, 1971; Thorne, 1972; Willis, 1996; or Barreno, 1991 and Egea & Alonso, 1996 for bryophytes and lichens), but the examples of animal species are more controversial, with many still unresolved biogeographical links between the fauna of the Iberian Peninsula, north Africa, the eastern Mediterranean, and Asia (see, e.g. López Martínez, 1989). Two main (not exclusive) hypotheses have been proposed to explain these distributions.

(1) Continuity of relict populations. The adjective 'relict' applies here to the persistence of a species despite the possibility of some changes in the surrounding areas, with the consequence of a generalized alteration in the composition of the broader regional communities. This would be the case for glacial boreo-alpine Pleistocene relicts in some mountains in southern Europe (e.g. Janssens, 1955;
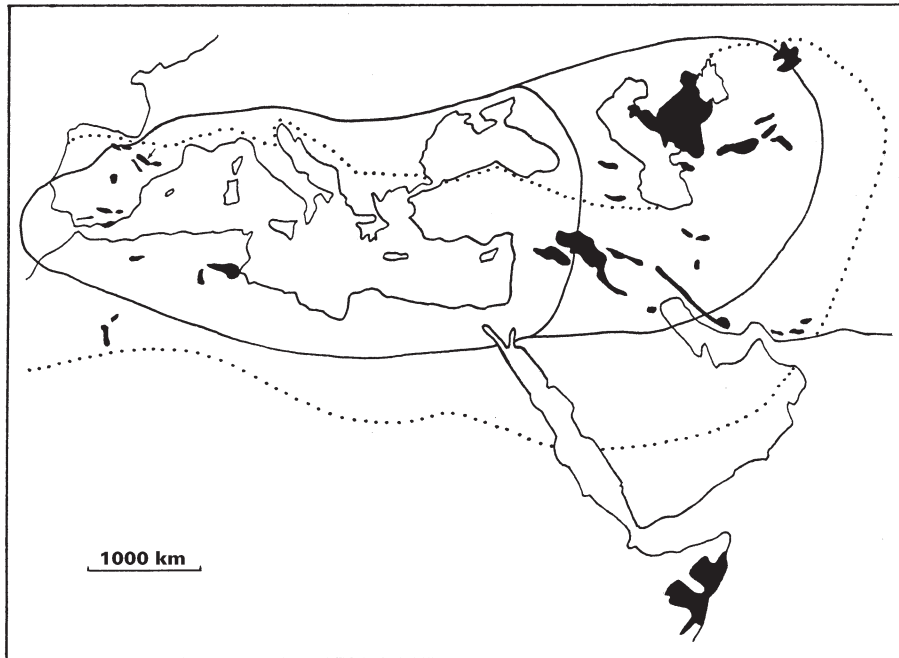
FIG. 1. Western Palaearctic region, with the distribution of gypsiferous soils (black areas) (from Alphen & Ríos Romero, 1971), the isoclimatic Mediterranean area (dotted line) (from Daget, 1977), and the biogeographical ranges (inner continuous line, Mediterranean distribution, outer continuous line, Mediterranean–Turanian distribution) (from Taglianti *et al.*, 1992). Arrow: position of the Monegros region. The areas of central Asia in which some species occur are not represented. Note the disjunct distribution of gypsiferous soils (see text).

Angus, 1983), or postglacial relicts in water bodies of periglacial thermokarstic origin (e.g. Foster, 1993; Bameul, 1994; Bilton, 1994). In both cases, a species is found in the limit of their distribution, inhabiting reduced patches of favourable habitat which in some key characteristics resemble their original optimum.

Supporters of this view claim that there has been enough continuity in the general ecological and climatic conditions in some parts of SW Europe (generally in the Iberian Peninsula) to allow the continuous presence of some species in the area since at least the Late Tertiary, and throughout all the Pleistocene glaciations. This is the hypothesis proposed by (among others) Brehm (1947) to explain the links between Iberian and Balkan cave-dwelling Crustacea (and other groups); Roth (1960) to explain the distribution of some sphecid wasps across the Mediterranean and the Turanian regions, with some forms apparently having closer affinities between both extremes (Iberia and the trans-Caspian deserts) than with intermediate forms in north Africa; Miracle (1982) to explain the presence of otherwise central-Asiatic species in the zooplanktonic Crustacea (specially Anostraca) of saline lagoons in closed basins in central Spain, among them those in the Monegros region; or the lepidoptera in steppe areas in the Ebro Valley and some other areas in east and south-east Spain (Domínguez *et al.*, 1997) (see also Oosterbroek & Arntzen, 1992 for a discussion of pre-Pleistocene trans-Mediterranean biogeographical relationships). A particular case would be the persistence of littoral species around the shores of former

Miocene seas in central Spain (e.g. Anadón, 1992; Coineau, 1994; Zaballos & Jeanne, 1994).

All these species would have had a wider original Late Tertiary distribution through most of the central Palaearctic region (paralleling that of some plants, Davis & Hedge, 1971; Thorne, 1972; Quézel, 1995), and originating during the salinity crisis of the Mediterranean basin in the Messinian (Hsü *et al.*, 1973). They would have persisted through the Pleistocene in the steppes of the eastern Mediterranean and central Asia, but also in steppe enclaves in western Europe, well removed from the eastern region (Brehm, 1947; see also Crusafont, 1958 for a discussion of the Miocenic mammalian fauna of NE Spain). The general framework of the distribution would be Mediterranean — Turanian (*sensu* Taglianti *et al.*, 1992), extending in some cases further east. This geographical region corresponds to what has been called the 'isoclimatic Mediterranean area' (Daget, 1977), a well-defined biogeographical domain for some groups of plants and lichens, considered to be the remnant of a Mesogean distribution during the Messinien (see, e.g. Barreno, 1991; Quézel, 1995) (Fig. 1). Some of the species have a more restricted Mediterranean range (*sensu* Taglianti *et al.*, 1992), occurring at both extremes of the Mediterranean sea but not in the trans-Caspian deserts of the Turanian region.

(2) Secondary colonization (or re-colonization). Although present climate and general environmental conditions between both sides of the disjunct distribution could be similar, allowing the existence of some common
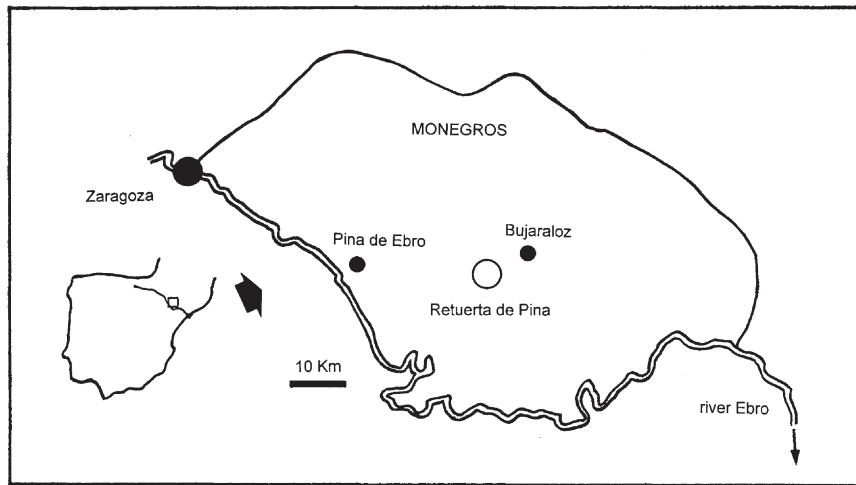
FIG. 2. Position of the Monegros and La Retuerta in the Iberian Peninsula.

species, these conditions would not have persisted across the Pleistocene. According to this view, the original Late Tertiary fauna of the region would have been displaced or eliminated together with the rest of the central and north European fauna, and the examples of disjunct distributions are due to recent, Holocenic colonization by species which are not known in intermediate areas because of lack of suitable habitats or lack of investigations.

Work by Russell Coope and collaborators has thoroughly demonstrated the ability of insect species to track suitable conditions across the Palaearctic region in relatively short times (e.g. Coope, 1979, 1995; see Elias, 1994 for a recent revision on the subject). This would allow for a recent origin of disjunct distributions, which would be due to ecological similarity and not to persistence in the area of relict communities across the Pleistocene. The present populations of these species in steppe-like areas in SW Europe would have migrated from the primary steppe areas of north Africa, the Middle East and northern Asia.

According to Baltanás *et al.* (1990) this could be the case of some Ostracoda occurring in steppe saline lagoons in the Iberian Peninsula and north Africa in the west, and in the eastern Mediterranean to the Caspian sea in the east. The present distribution would be the result of recent colonization (re-colonization?) of these areas by migratory waterfowl between Asia, Africa, and Europe. This would also be the case for the steppe birds in central and SE Spain (Goriup, 1988); or the anostracan (Crustacea) *Streptocephus torvicornis* (Waga) (Dumont *et al.*, 1995).

Although the presence of the same species assemblages in disjunct areas with the same general ecological conditions across the Palaearctic does not constitute evidence of an old distributional pattern, the phylogenetic relationships of the species with restricted distributions can be used to reconstruct past biogeographical links (Morrone & Crisci, 1995). The evolutionary stability of insect species during the Pleistocene is now widely accepted (see, e.g. Coope, 1979; Angus, 1983; Elias, 1994),

being largely attributed to the dynamics imposed by the frequent and rapid climatic shifts during this period, which did not allowed the persistence of isolated populations. The same dynamics may, however, result in changes in genetic variability or genomic organization, albeit at an intraspecific level (Hewitt, 1996). This has two major implications. First, it allows the disjunct distribution of the same species across the Palaearctic to be old in origin (although, of course, it does not mean that they are old). Secondly, when evolutionary change *has* taken place, and the disjunct distributions are not of the same species but closely related species, this can be taken as evidence of an old link. Of particular significance are the phytophages insects feeding on plants with disjunct distributions, and the parasitoids of such species.

During the last 5 years one of the authors (JBZ) has intensively studied the insect communities in a steppe habitat on gypsum grey soils in the Monegros region, in particular in La Retuerta de Pina (Zaragoza, NE Spain) (Fig. 2). This is one of the traditional areas with known examples of disjunct distributions both of plants and animals (e.g. Braun-Blanquet & Bolòs, 1957; Llimona, 1973; Miracle, 1982; Baltanás *et al.*, 1990). Many new examples of both species and species groups of insects with a disjunct distribution between the central Iberian and the eastern Mediterranean and Asiatic steppes were found.

The aim of this paper is to evaluate the possible evidence supporting the hypothesis of the continuity of at least some insect species associated with steppe habitats in the central area of the Ebro Valley through the Pleistocene. In this sense, the specific question to be addressed is if enough examples of disjoint distributions are known to made alternative *ad-hoc* explanations highly improbable. The paper does not study the biogeography of particular monophyletic groups, the hypothesis under consideration has a predominantly historical character, being difficult — if not impossible – to test rigorously (see Andersson, 1996 for a discussion of hypotheses testing in historical biogeography). However, its plausibility can be evaluated

through the recognition of similar patterns in the range of extant species or closely related species groups.

MATERIALS AND METHODS

Study area

The Monegros region, with a total extension of ≈ 2500 km^2, is situated in the centre of the Ebro depression, between the rivers Gállego, Ebro, Cinca, Isuela and Flumen (Fig. 2). The general climate is Mediterranean, although continental and arid, due to the isolating effect of the Pyrenees in the north, the Catalonian littoral mountains in the east, and the Iberian system in the south and the west. The usual annual temperature range is more than 50 °C (from -10 °C to more than 40 °C), with maximum recorded values of more than 60 °C in Zaragoza (Braun-Blanquet & Bolòs, 1957), and frost for up to seven months a year (Ochoa, 1982). Annual precipitation in the area ranges from 200 to 400 mm (concentrated in spring and autumn), with a total water deficit of more than 300 mm. Dominant winds have NW and NE direction, and are predominantly dry. The altitude of the area ranges from about 200–800 m. The only natural water bodies are temporary saline lagoons in closed basins ('saladas') (see, e.g. Baltanás *et al.*, 1990; Santamaría *et al.*, 1992) and some temporary streams ('barrancos' and 'vales'). The central area has poorly developed semidesertic gypsum grey soils, with a more calcareous composition in the periphery (Gabaldón, 1995). There are no signs of strong erosion, the Monegros being considered a pre-Pleistocene fossil landscape by some authors (e.g. Terradas, 1986). The present general chemical and soil patterns of evaporite formation are thought to be similar (albeit in a different scale) to those of the Late Miocene basin (Anadón, 1992).

These climatic and soil conditions determine the existence of vegetation cover dominated in altitudes under 400 m by clear woodland of 'sabina albar' (*Juniperus thurifera* L., Cupressaceae), characteristic of the association *Juniperetum phoeniceo-thuriferae* (Br.-Bl. & Bolòs) Rivas-Martínez (Rivas-Martínez, 1987). The undergrowth is formed by different associations belonging to *Gypsophilion hispanicae* (Br.-Bl.) Br.-Bl. & Bolòs and *Agropyro-Lygeion* Br.-Bl. & Bolòs. Detailed composition of the plant communities is determined by changes in microclimatic conditions due to differences in altitude, orientation, and soil composition (Braun-Blanquet & Bolòs, 1957; Terradas, 1986). An important characteristic of the area is the frequent occurrence of thermal inversions during the winter, resulting in a more thermophilous flora and fauna at higher altitudes. The dominant species of these associations are steppe grasses (*Stipa* spp., *Lygeum spartum* L. and others) and sclerophytous shrubs (*Helianthemum* spp., *Ononis tridentata* L., *Rosmarinus officinalis* L. and others) (Braun-Blanquet & Bolòs, 1957; Terradas, 1986).

The phytogeography of the Monegros region has been studied in detail by (among others) Braun-Blanquet & Bolòs (1957), Ochoa (1982), and Terradas (1986) (see also Blanché & Molero, 1986 for the phytogeography of the vegetation of the saline lagoons). The flora is essentially Mediterranean in origin, with strong links with north Africa, but there is an important component of Ponto-Turanian or Sarmantian species, which are thought to have reached central Iberia in the Late Miocene through north Africa or central Europe (see Discussion for some examples).

Due to human disturbance the natural vegetation has almost completely disappeared from the region, being confined to some reduced relict areas. The largest of these enclaves is La Retuerta de Pina, a patch of 20 km^2 in Pina de Ebro, province of Zaragoza (between U.T.M. 10×10 km reference grid squares 30TYL29 and 30TYL39). Gypsum grey soils predominate in La Retuerta, and the general climatic conditions are those described for the Monegros region above.

Geological and historical background of the central Ebro valley

The Ebro valley was a closed basin separated from the sea by the Catalonian littoral mountains from the end of the Eocene until the end of the Miocene (Uchupi, 1988; Nelson & Maldonado, 1990). During most of the Miocene the more continental arid conditions, coupled with isostatic subsidence, resulted in the formation of strong deposits of evaporites on the central area of the basin (Uchupi, 1988; Guimerà, 1992), in coincidence with the Messinian salinity crisis of the Mediterranean basin (Hsü *et al.*, 1973). Gypsiferous soils with similar characteristics are found in other Mediterranean areas of the Iberian Peninsula, northern Africa, and the eastern Mediterranean region (Alphen & Ríos Romero, 1971, see Fig. 1), in coincidence with some of the distributional ranges discussed below. The opening of the Gibraltar Straits at the beginning of the Pliocene restored the Mediterranean-Atlantic interchange, with the consequence of a less dry overall climate and the amelioration of the conditions in most of the basin (Suárez *et al.*, 1992). During the early Pliocene (3.2 Ma) the general Mediterranean climatic rhythm was established in SW Europe, with summer drought and precipitation concentrated mostly in spring and autumn (Suc, 1984).

When considering the possibility of the persistence of some species in southern Europe throughout the Pleistocene it must be remembered that most of the sites for which fossil information is available are from central and northern Europe, which were certainly more severely affected by climatic changes. On the contrary, extensive areas in NE Spain were always free of ice, the glacials being restricted to mountains systems over 1500 m, and some adjacent valleys (Jalut *et al.*, 1982; Guimerà, 1992). Although extensive climatic changes have been documented in some parts in Spain (see, e.g. Turner & Hannon, 1988; Beaulieu *et al.*, 1992; Reille & Lowe, 1993), recent work clearly demonstrates that the changes during the Pleistocene in the southern Mediterranean region were less dramatic than previously thought, and there is increasing evidence of the persistence of a landscape formed by dry steppe and open woodland throughout the glaciations even in the mountains (e.g. Suc *et al.*, 1995; Thinon *et al.*, 1996).

There has been some controversy about the possibility of the persistence of naturally deforested (or scarcely afforested) steppe areas in the Iberian Peninsula across the

Pleistocene. Early authors considered the steppes to be natural (e.g. Willkomm, 1852), although subsequently, and especially due to the influence of Del Villar (1915), they were considered to be anthropic in origin (see, e.g. Goriup, 1988). The more recent tendency is, notwithstanding the acknowledgement of the anthropic origin of some of the steppe-like habitats, to consider the possibility of the persistence of areas with natural steppes across the Pleistocene, due to the special conditions created by the orographic diversity and the soil characteristics (e.g. Terradas, 1986; González Bernáldez, 1989; Suárez *et al*., 1992; Blondel & Vigne, 1993; Suc *et al*., 1995; Willis, 1996). The view of a dense forest covering the central Ebro basin during most of the Pleistocene has progressively changed towards a naturally clear, low density woodland, with cold dry steppes during the glacial maxima, in which full-glacial floras with cold dry steppe vegetation with *Artemisia* (Compositae) and Chenopodiaceae were common in most of southern Europe (Turner & Hannon, 1988; de Beaulieu *et al*., 1992; Reille & Lowe, 1993; Suc *et al*., 1995; Willis, 1996). Despite the retreat of more thermophilous species to refugia there was a continued persistence of dry *Artemisia* and *Ephedra* steppes with sparse woodland (mainly *Juniperus* and *Pinus*) in the centre of the Iberian Peninsula (Terradas, 1986; Suárez *et al*., 1992). The climatic amelioration after the glacial maxima reduced the geographical extension of these areas with natural open forest, being nowadays mainly confined to arid enclaves on gypsum or saline soils in central and SE Spain. There was not a uniform pattern across southern Europe in changes in vegetation due to the Late Pleistocene climatic amelioration, and local factors can account for the different, more recent history of individual floras (Turner & Hannon, 1988; de Beaulieu *et al*., 1992; Blondel & Vigne, 1993; Suc *et al*., 1995; Willis, 1996).

Material studied

All the material studied was collected in La Retuerta de Pina and some nearby similar habitats by JBZ between 1990 and 1995, and sent to specialists of the different groups for systematic work (see Acknowledgments). Different collecting methods were used in all the recognized microhabitats: Moericke traps, Malaise traps, light traps, pitfall traps, Wilkening traps, emergence traps, baited traps, interception traps, coloured dishes, Berlese funnels, sweeping nets, and direct visual collecting (see, e.g. Bächli & Blasco-Zumeta, 1995 and Ribes *et al.*, 1997 for more details of the collecting methodology).

More than 4000 species of invertebrates have so far been identified, most of them insects (Blasco-Zumeta, 1996 and unpublished data). Although the study of some groups is still not complete (Table 1), as a result of this work more than one hundred species new to science have been described, most of them so far known only from the study area. The zoogeographical analysis of the groups in which most of the species have been studied reveals a similar general composition of the fauna, with most species having a Mediterranean-type distribution. For instance, in Heteroptera (242 spp.), about 70% of the species have

Mediterranean distributions, 12% are Iberian or Ibero-provenzal endemics, only 1.2% are so far only known from the Monegros region, and there are only three species with west–east disjunct distributions (see results) (Ribes *et al*., 1997). Other groups have similar compositions (unpublished data).

Two different sources of evidence were considered for this study: the disjunct distribution of the same species, and the disjunct distribution of vicariant species (or subspecies). It must be noted that the starting point was the study of the relationship between areas, not of a particular monophyletic group, and in consequence the analysis was restricted to either individual species or vicariant species groups previously recognized in the areas under examination. In the analysis of disjunct distributions, the lower the taxonomic rank of the taxa involved, the more detailed the conclusions than can be obtained (Thorne, 1972).

Only steppe species or vicariant species groups with a clear gap between their western and eastern ranges were included in the study. The precise delimitation of the size of this gap is, however, problematic (see Discussion), specially in groups for which the knowledge of their distribution in north Africa is still very poor. Some species with isolated populations in intermediate localities were included, because most of these intermediate localities are relict steppe or arid habitats. The boundary between the western and eastern Mediterranean basins was considered to be the Italian peninsula, Sicily and Tunisia, following Taglianti *et al*. (1992).

Results are divided in two main sections: species with disjoint distributions, and vicariant species or species groups with disjoint distributions. Iberian endemic species with uncertain phyletic relationships feeding on steppe plants or insects which had disjoint distributions themselves were also included, as they provide strong evidence favouring the hypothesis of the continued presence in the area of their hosts. Within each section species are grouped by order and family (see Tables 2 and 3), and numbered for later reference in the text and Tables. Unpublished new records given in the results section are specifically noted to avoid confusion with already published information.

RESULTS

Steppe species with disjoint distributions (Table 2)

Coleoptera

1. *Sitona callosus* Gyllenhal 1834 (Curculionidae). Known to occur in Monegros, and in the steppes from Poland and the Balkans to China (province of Sinkiang) (Dieckmann, 1978; Velázquez & Blasco-Zumeta, 1994).
2. *Hypocacculus (Colpellus) biskrensis* (Marseul 1878) (Histeridae). Known from Monegros, Algeria (the type locality), Tunisia, Crete, Greece, Middle East, Turkmenistan, Uzbekistan, Tajikistan, India and Sudan (Gomy, 1995).

Diptera

3. *Calamoncosis stylifera* Nartshuk 1971 (Brachycera,

TABLE 1. Number of families and species occurring in Retuerta de Pina in each of the taxonomic groups in which species or species groups with disjunct distributions were found (with the exception of 21, 35, and 63, which are from surrounding areas in the Monegros). Taxa for which less than 80% of the collected specimens have been identified are marked with stars.

Order	Suborder/Superfamily	Family	No. spp. with disjunct distributions	Species ref. no.
Cl. Acari	Actinedida 24 spp.	Eriophydae 11 spp.	1	35
Acarimorfa 108* spp., 44 f.		Coleoptera	1	36
501* spp., 52 f.		Chrysomelidae 54* spp.		
		Curculionidae 59* spp.	2	1, 37
		Histeridae 19* spp.	1	2
Diptera 758* spp., 61 f.	Brachycera 567* spp.	Chloropidae 16* spp.	1	3
		Heleomycidae 18 spp.	3	4, 38, 39
		Hybotidae 19 spp.	1	40
		Phoridae 35* spp.	1	5
		Pipunculidae 22 spp.	8	6–10, 41–43
		Scatophagidae 3 spp.	1	11
		Tachinidae 82 spp.	2	12, 13
		Tephritidae 24 spp.	1	44
		Xenasteiidae 1 sp.	1	45
	Nematocera 191* spp.	Cecidomyiidae 19 spp.	1	46
		Ceratopogonidae 34 spp.	2	14, 15
		Sciaridae 38* spp.	2	47, 48
Heteroptera 242 spp., 28 f.		Miridae 74 spp.	2	16, 17
		Reduviidae 19 spp.	1	49
		Tingidae 14 spp.	1	18
Homoptera 170* spp., 14 f.	Psylloidea 38 spp.	Psyllidae 29 spp.	2	20, 21
	Cicadelloidea 34* spp.	Cicadelidae 34* spp.	2	19, 50
Hymenoptera 759* spp., 49 f.	Vespoidea 31 spp.	Eumenidae 25 spp.	2	57, 58
	Chalcidoidea 474 spp.	Chalcididae 25 spp.	2	22, 51
		Encyrtidae 65 spp.	2	23, 24
		Eulophidae 100 spp.	2	25, 26
		Eurytomidae 11 spp.	2	52, 53
		Ormyridae 8 spp.	2	54, 55
		Perilampidae 10 spp.	1	27
		Pteromalidae 154 spp.	1	28
		Torymidae 23 spp.	1	56
Lepidoptera 467 spp., 42 f.	Heterocera 419 spp.	Geometridae 86 spp.	3	29–31
		Lasiocampidae 6 spp.	1	59
		Noctuidae 151 spp.	3	32, 60, 61
	Rhopalocera 48 spp.	Pieridae 10 spp.	1	33
Neuroptera 41 spp., 9 f.		Coniopterygidae 12 spp.	1	34
Psocoptera. 35 spp., 11 f		Elipsocidae 9 spp.	1	62
Thysanoptera 60* spp., 3 f.	Terebrantia 41* spp.	Thripidae 30* spp.	1	63

Chloropidae). Known from Monegros and Mongolia (De Bruyn & Blasco-Zumeta, 1994).

4. *Oecothea ushinskii* Gorodkov 1959 (Brachycera, Heleomycidae). Known from Monegros, the Crimean Peninsula, Turkmenistan and Tajikistan (Carles-Tolrà, 1993).

5. *Razorfemora nussbaumi* Disney 1990 (Brachycera, Phoridae). Known from Monegros in the west and Israel in the east (Disney, 1994).

6–10. *Eudorylas fluviatilis* (Becker 1900) (Brachycera, Pipunculidae) (6), known only from the Monegros and the Canary Islands in the west, and Egypt, Israel, and the Caucasus in the west (De Meyer, 1995, 1997); *Tomosvaryella argyratoides* De Meyer 1995 (7) and *T. trichotibialis* De Meyer 1995 (8), known only from the Monegros and Israel; and *T. docta* De Meyer 1995 (9) and *T. freidbergi* De Meyer

1995 (10), known only from the Monegros, the Sinai desert, and Israel (De Meyer, 1995, 1997).

11. *Scathophaga fluvialis* (Rondani 1867) (Brachycera, Scatophagidae). Known from Monegros and Turkmenistan (Nelson & Blasco-Zumeta, 1993). The species was described from Parma (Italy), but it has not been recorded again, and before its discovery in Monegros its presence in the west Palaearctic was considered dubious (Nelson & Blasco-Zumeta, 1993).

12–13. *Engeddia multisetosa* Kugler 1977 (12) and *Dionomelia hennigi* Kluger 1978 (13) (Brachycera, Tachinidae). Known from Monegros in the west and Israel in the east (Tschorsnig *et al.*, 1997).

14–15. *Culicoides brevifrontis* Smatov & Isimbekov 1971 (14) and *C. kurensis* Dzhafarov 1962 (15) (Nematocera, Ceratopogonidae). Known from Monegros, Saudi Arabia

TABLE 2. Steppe species occurring in the Monegros region with disjoint western − eastern distributions.

	Species	Family	Western Mediterranean distribution	Eastern Mediterranean distribution	Turanian distribution	Host
	Coleoptera					
1	*Sitona callosus*	Curculionidae	Monegros	Eastern Europe, the Balkans	trans-Caspian republics, central Asia, China	
2	*Hypocacculus biskrensis*	Histeridae	Monegros, Algeria, Tunisia	Crete, Greece, Middle East	Turkmenistan, Uzbekistan, Tajikistan, India, Sudan	
	Diptera					
3	*Calamoncosis stylifera*	Chloropidae	Monegros		Mongolia	
4	*Oecothea ushinskii*	Heleomycidae	Monegros	Crimea	Turkmenistan, Tajikistan	
5	*Razorfemora nussbaumi*	Phoridae	Monegros	Israel		
6	*Eudorylas fluviatilis*	Pipunculidae	Monegros, Canary Islands	Egypt, Israel	the Caucasus	
7	*Tomosvaryella argyratoides*	Pipunculidae	Monegros	Israel		
8	*T. trichotibialis*	Pipunculidae	Monegros	Israel		
9	*T. docta*	Pipunculidae	Monegros	the Sinai desert, Israel		
10	*T. freidbergi*	Pipunculidae	Monegros	the Sinai desert, Israel		
11	*Scathophaga fluvialis*	Scathophagidae	Monegros, Italy		Turkmenistan	
12	*Engeddia multisetosa*	Tachinidae	Monegros	Israel		
13	*Dionomelia hennigi*	Tachinidae	Monegros	Israel		
14	*Culicoides brevifrontis*	Ceratopogonidae	Monegros		Saudi Arabia, Kazakhstan	
15	*C. kurensis*	Ceratopogonidae	Monegros, Morocco	Cyprus, Turkey, Israel	Iran, Iraq, Azerbaijan, Turkmenistan	
	Heteroptera					
16	*Orthotylus arabicus*	Miridae	Monegros	Syria, Israel	Iraq, Arabian peninsula, Eritrea, Somalia	
17	*O cupressi*	Miridae	Monegros, Barcelona, France	Turkey		
18	*Campylosteira heissi*	Tingidae	Monegros		Iraq, Saudi Arabia	
	Homoptera					
19	*Rhopalopyx brevis*	Cicadellidae	Monegros		Kazakhstan	
20	*Cacopsylla saligna*	Psyllidae	Monegros		Kazakhstan	
21	*Eurotica distincta*	Psyllidae	Monegros		Caucasus to Mongolia	*K. ceratoides*
	Hymenoptera					
22	*Philomides paphius*	Chalcididae	Monegros, Sicily	Cyprus, the Balkans	the Caucasus, Turkmenistan, Kazakhstan	
23	*Monstranusia mirabilissima*	Encyrtidae	Monegros	former Yugoslavia	former U.R.S.S., Afghanistan, Pakistan, South-Africa	
24	*Semen apterum*	Encyrtidae	Monegros	Czech Republic, Moldavia, Crimea	W Russia	
25	*Platyplectrus bouceki*	Eulophidae	Monegros	Czech Republic, Hungary, Moldavia, Turkey		
26	*Kolopterna kohatensis*	Eulophidae	Monegros		Pakistan	
27	*Chrysomalla roseri*	Perilampidae	Monegros	Germany, Czech Republic, Hungary	Kazakhstan	
28	*Mesopolobus szelenyii*	Pteromalidae	Monegros, possibly Tenerife		Azerbaijan, Ukraine	
	Lepidoptera					
29	*Cinglis humifusaria*	Geometridae	Monegros, other Iberian steppes		Asiatic steppes	*A. herba-alba*
30	*Narraga nelvae*	Geometridae	Monegros, other Iberian steppes		Asiatic steppes	*A. herba-alba*
31	*Eupithecia variostrigata*	Geometridae	Monegros, other Iberian steppes		Asiatic steppes	*A. herba-alba*
32	*Cardepia sociabilis*	Noctuidae	Monegros, other Iberian steppes	Syria	Turkmenistan	*Artemisia* spp.
33	*Zegris eupheme*	Pieridae	Monegros	Turkey, Syria	Iran	
	Neuroptera					
34	*Helicoconis panticosa*	Coniopterygidae	Monegros, central Pyrenees	Turkey		

TABLE 3. Vicariant species groups occurring in the Monegros region with western − eastern distributions, and endemic species on hosts with disjoint distributions.

	Western Species	Family	Distribution	Host	Vicariant Eastern Species	Distribution	Host
	Acari						
35	*Aceria zumetae*	Eriophyidae	Monegros	*K. ceratoides*	*Aceria sarcobati*	north-America	
	Coleoptera						
36	*Cryptocephalus ingamma*	Chrysomelidae	central Ebro Valley	*A. herba-alta*	spp of the subgenus	E Europe, steppes of central Asia	
37	*Theodorinus hispanicus*	Curculionidae	Monegros, Almeria, Madrid	*E. nebrodensis*	*T. transcaucasicus* *T. multidentatus*	Caucasus Turkmenistan, Kazakhstan	*Ephedra spp* *Ephedra spp*
	Diptera						
38–39	*Schroederella hispanica* *S. bifida*	Heleomyzidae	Monegros		spp of the genus	5 spp east Palaearctic steepes 2 spp Hungary 1 sp Palaearctic	
40	*Platypalpus monegrensis*	Hybotidae	Monegros		*P. agnitus* *P. thyamis*	Israel Algeria	
41–42	*Eudorylas dilatatus* *Eudorylas turnidus*	Pipunculidae	Monegros		*E. imitator* *E. sinaiensis*	Israel the Sinai desert	
43	*Tomosvaryella hispanica*	Pipunculidae	Monegros		*T. parakuthyi*	Israel, the Sinai desert	
44	*Rhagoletis zernyi*	Tephritidae	Monegros, S. Aragón	*J. thurifera*	*R. flavigenualis*	Turkey	*J. excelsa*
45	*Xenasteia* cf. *excellens*	Xenasteiidae	Monegros, Tunisia		1 Palaearctic sp of the genus other spp of the genus	Israel Pacific & Indian oceans	
46	*Etsuhoa thuriferae*	Cecidomyiidae	Monegros, central Spain, Morocco	*J. thurifera*	*E. okayamana* *E. tjanshanica* *E. severtzovi* *E. renifolia*	Japan Kazakhstan Kazakhstan Kazakhstan	*J. rigida* *J. semiglobosa* *J. semiglobosa* *J. pseudosabina*
47–48	*Parapnyxia hispanica* *P. intermedialis*	Sciaridae	Monegros		*P. germanica* spp of the genus	Germany (gypsum soils) Turkmenistan, Kazakhstan	
	Heteroptera						
49	*Ploiaria putoni*	Reduviidae	Monegros, E Iberia, S France		*P. katznelsoni* *P. turkestanica*	Israel Kazakhstan	
	Homoptera						
50	*Dudalus javieri*	Cicadellidae	Monegros, other Iberian steppes		*D. pallidus* *D. junatovi*	Slovaquia central Siberia	

contd

TABLE 3. *contd*

	Western Species	Family	Distribution	Host	Vicariant Eastern Species	Distribution	Host
	Hymenoptera						
51	*Psilochalcis frontalis*	Chalcididae	Monegros		*Cephalochalcidia capitata* *C. levis*	Turkmenia Turkmenia	*E. nebrodensis*
52	*Eurytoma gallephedrae*	Eurytomidae	Monegros, Madrid	*E. nebrodensis*	*E. flaveola*	central Asia	
53	*Nikanoria ephedrae?*	Eurytomidae	Monegros, W France?	*E. nebrodensis* galls	*N. metallica*	Hungary, Croatia, Czechoslovakia, Moldavia, Serbia, central Asia	
54	*Ormyrus monegricus*	Ormyridae	Monegros	*Stefaniola salsolae*	spp of the genus *O. oranensis* *O. ardahanensis*	steppes of central Asia Algeria Turkey	
55	*Ormyrus cupreus*	Ormyridae	Monegros	*Eurytoma gallephedrae*	*O. orientalis*	Oriental region, Palaearctic (introduced?)	
56	*Ameromicrus* sp.n.	Torymidae	Monegros		spp of the genus	central Europe to central Asia.	
57	*Paragymnomerus spiricornis*	Eumenidae	central Ebro valley, Italy, the Caucasus		*P. spiricornis turanicus*	E Turanian region, central Asia.	
58	*Ischnogasteroides picteti*	Eumenidae	Monegros, E Spain, S France		*I. picteti tenuis*	Turkmenia, Kazakhstan, Mongolia	
	Lepidoptera						
59	*Pachypasa limosa*	Lasiocampidae	Monegros, Iberia, NW Africa	*J. thurifera*	*P. otus*	Asia	*Juniperus & Cupressus*
60	*Cucullia bubaceki*	Noctuidae	Monegros, Iberia	*A. herba-alta*	*C. argentina*	Irano-Turanian region	*A. herba-alta*
61	*C. achilleae*	Noctuidae	Monegros, Iberia	*A. herba-alta*	*C. boryphora*	Irano-Turanian region	*A. herba-alta*
	Psocoptera						
62	*Hemineura blascoi*	Elipsocidae	Monegros		*H. trudiae*	Israel	
	Thysanoptera						
63	*Blascothrips zumetai*	Thripidae	Monegros	*K. ceratoides*	?	?	

(Bahrein) and Kazakhstan the former, and Monegros, Morocco, Cyprus, Turkey, Israel, Iran, Iraq, Azerbaijan and Turkmenistan the latter (Smatov & Isimbekov, 1971; Delécolle *et al.*, in press).

Heteroptera

16–17. *Orthotylus (Melanotrichus) arabicus* Wagner 1962 (16) (Miridae). Known from Monegros in the west, and Iraq, the Arabian peninsula, Eritrea, Somalia, Syria and Israel in the east (Ribes, 1993). *O. (Pinocapsus) cupressi* Reuter 1883 (17), another mirid, is known from the Monegros, Barcelona and France (on different species of *Cupressus* and *Juniperus*) in the west, and Turkey in the east (Ribes *et al.*, 1997).

18. *Campylosteira heissi* Péricart 1980 (Tingidae). The species is known from Monegros in the west, and Iraq and Saudi Arabia in the east (Ribes, 1993).

Homoptera

19. *Rhopalopyx brevis* Emeljanov 1962 (Cicadelloidea, Cicadellidae). Known from Monegros and Kazakhstan (della Giustina et Blasco-Zumeta, in prep.).

20–21. *Cacopsylla saligna* (Loginova 1966) (Psylloidea, Psyllidae) (20). Known from Monegros and Kazakhstan (Lauterer & Burckhardt, 1994). *Eurotica distincta* Loginova 1960 (21), another psyllid, feeds on *Krascheninnikovia ceratoides* (L.) Gueldenst. (Chenopodiaceae) in the Monegros (D. Burckhardt, unpublished data). The species is known to occur from the Caucasus to Mongolia on the same host (Gegechkori & Loginova, 1990).

Hymenoptera

22. *Philomides paphius* Haliday 1862 (Chalcidoidea, Chalcididae). Found in Monegros, Sicily, Cyprus and the Balkans in the Mediterranean; and in Turkmenistan, west Kazakhstan and further sites in the Caucasus in Asia (Askew, 1995). The genus is included, with the Afro-tropical *Aperilampus* Walker, in the subfamily Philomidinae, a group of parasitoids of uncertain relationships (Askew, 1995).

23–24. *Monstranusia mirabilissima* Trjapitzin 1964 (23) (Chalcidoidea, Encyrtidae). Known from Monegros, the former Yugoslavia, the former U.S.S.R., Afghanistan, Pakistan and South Africa (R.R. Askew, unpublished data). *Semen apterum* Hoffer (24) is another encirtid known from Monegros, the Czech Republic, Moldavia, Crimea and W Russia (R.R. Askew, unpublished data).

25–26. *Platyplectrus bouceki* (Erdös 1966) (25) and *Kolopterna kohatensis* Graham 1987 (26) (Chalcidoidea, Eulophidae), known from Monegros, the Czech Republic, Hungary, Moldavia, and Turkey the former (R.R. Askew, unpublished data); and Monegros and Pakistan the later (Askew, 1997).

27. *Chrysomalla roseri* Förster 1859 (Chalcidoidea, Perilampidae). Known from Monegros, Germany, the Czech Republic, Hungary and Kazakhstan (R.R. Askew, unpublished data).

28. *Mesopolobus szelenyii* Boucek 1974 (Chalcidoidea, Pteromalidae). Found in Monegros and possibly Tenerife (the specimens had some morphological differences) in the

west, and Azerbaijan and Ukraine in the east (Askew, 1993).

Lepidoptera

29–31. *Cinglis humifusaria* (Eversmann 1837), *Narraga nelvae* (Rothschild 1912), and *Eupithecia variostrigata* Alpheraky 1878 (Heterocera, Geometridae), are species living on *Artemisia herba-alba* Asso (Compositae), with disjoint populations in the eastern Iberian steppes (including Retuerta de Pina, V.M. Redondo unpublished data) and the Asiatic steppes (Domínguez *et al.*, 1997).

32. *Cardepia sociabilis* (Graslin 1850) (Heterocera, Noctuidae) lives on *Artemisia* species in the Monegros and other Iberian steppes, and in Syria and Turkmenistan (Domínguez *et al.*, 1997; V.M. Redondo, unpublished data).

33. *Zegris eupheme* (Esper 1782) (Rhopalocera, Pieridae). Known to occur in Monegros, and in the steppes of Turkey, Syria and Iran (Domínguez *et al.*, 1997; V.M. Redondo, unpublished data).

Neuroptera

34. *Helicoconis panticosa* Ohm 1965 (Coniopterygidae). Described from the central Pyrenees, it also occurs in the Monegros (V. Monserrat, unpublished data) and Turkey (Monserrat, 1994).

Vicariant species groups with western − eastern distributions, and endemic species on hosts with disjoint distributions (Table 3)

Acari

35. *Aceria zumetae* Boczek & Petanovici 1994 (Actinedida, Eriophyidae) is found on *Krascheninnikovia ceratoides* in Monegros. According to M. Skuhravá (unpublished data) this is the only known gall in *K. ceratoides*. The species is most close to *Aceria sarcobati* Keifer 1962 (Bockzek & Petanovic, 1994), a North-American species.

Coleoptera

36. *Cryptocephalus (Asiopus) ingamma* Pic 1908 (Chrysomelidae). Described from the central Ebro Valley (near Zaragoza), and common in the Monegros region. The other species in the subgenus are distributed through eastern Europe and the steppes of central Asia (Petitpierre, 1993).

37. *Theodorinus hispanicus* Colonnelli 1995 (Curculionidae) (37), recently described from Almería (SE Spain), feeds on *Ephedra nebrodensis* Tineo in Guss. (= *E. major* Host) (the Joint Pine) in Monegros, and also in an area with gypsiferous soils around Madrid (M.A. Alonso Zarazaga, unpublished data). The genus has three know species, *T. hispanicus*, *T. transcaucasicus* Korotayaev 1981 from the Caucasus, and *T. multidentatus* Pic 1914, from Turkmenistan and Kazakhstan, all of them living on species of *Ephedra* (Colonnelli, 1995).

Diptera

38–39. The genus *Schroederella* (Brachycera, Heleomyzidae) has a pre-eminently eastern distribution, with five species in the western Palaearctic (Papp & Carles-Torlá, 1994). Among the later, two are so far known only from Retuerta de Pina (*S. hispanica* Papp & Carles-Torlá 1994–38

− and *S. bifida* Papp & Carles-Torlá 1994−39), two are Hungarian endemics (*S. minuta* Papp & Carles-Torlá 1994 and *S. hungarica* Papp & Carles-Torlá 1994), and one has a widespread Palearctic distribution, reaching Mongolia in the east (*S. iners* (Meigen 1830)) (Papp & Carles-Torlá, 1994).

40. *Platypalpus monegrensis* Grootaert 1995 (Brachycera, Hybotidae). So far only know from the Monegros. It is mostly related to *P. agnitus* (Collin 1960) and *P. thyamis* (Séguy 1942) from Israel and Algeria repectively (Grootaert, 1995).

41–43. Two species of the genus *Eudorylas* (41 & 42) (Brachycera, Pipunculidae) described from the Monegros region form a species group with *E. imitator* De Meyer 1995 and *E. sinaiensis* De Meyer 1995, from Israel and the Sinai desert, respectively (De Meyer, 1997). Another species of *Tomosvaryella* (43) (Pipunculidae) described from Monegros is most closely related to *T. parakuthyi* De Meyer 1995, also from Israel and the Sinai desert (De Meyer, 1995, 1997).

44. *Rhagoletis zernyi* Hendel 1927 (Diptera, Brachycera, Tephritidae) is another endemic species from Monegros and Albarracín (the type locality, in southern Aragón), thought to be entirely depend on *Juniperus thurifera* (Merz & Blasco-Zumeta, 1995). Its closest relative is *R. flavigenualis* Hering 1958, a species living in Turkey (in south Anatolia, Antalya-Kas and Katrandag) on the fruits of the closely related species *Juniperus excelsa* (Hering, 1958).

45. *Xenasteia* cf. *excellens* (Papp 1980) (Brachycera, Xenasteiidae). Know from Monegros in the west, and Tunisia in the central Mediterranean (Carles-Tolrà, 1995). It is the only European species of this monogeneric family, which in the Palaearctic region has two species, *X. excellens* and another species in Israel (the other members of the genus − seven species − are found in the Pacific and Indian oceans, Carles-Tolrà, 1995). However, the identity of the species needs to be confirmed, it possibly representing a new taxon, in which case the two species form a complex in the west-central Mediterranean, with a third species in Israel (Carles-Tolrà, 1995).

46. *Etsuhoa thuriferae* Skuhravá 1995 (Nematocera, Cecidomyiidae) forms galls in *Juniperus thurifera* in Monegros, Soria (central Spain), and Morocco (although adults have been recovered from galls in the Monegros only). *E. thuriferae* is the first west Palaeartic species of the genus, the other species (four) have eastern distributions: *E. okayamana* Inouye 1959 in Japan; and *E. tjanshanica* Marikovskij 1969, *E. severtzovi* Marikovskij 1969, and *E. renifolia* Fedotova 1985 in Kazakhstan (Skuhravá, 1995). The eastern species occur associated with three different hosts of the same genus *Juniperus*, *J. rigida* Sieb. & Zucc. (*E. okayamana*), *J. semiglobosa* Rgl. (*E. tjanshanica* and *E. severtzovi*), and *J. pseudosabina* Fisch. et Mey (*E. renifolia*).

47–48. *Parapnyxia hispanica* Mohrig & Blasco (1995) (47) and *P. intermedialis* Mohrig & Blasco 1995 (48) (Nematocera, Sciaridae). So far known only from Monegros. Previous species of the genus are endemic to the deserts east of the Caspian sea (Karakumy and Kyzylkum, in Turkmenistan and Kazakhstan), with the only exception of one German species ocurring in arid microclimates with gypsum soils (*P. germanica* Mohring 1970). All species have more or less micropterous males, and all known females are apterous, living in the soil (Mohring & Blasco-Zumeta, 1995).

Heteroptera

49. *Ploiaria putoni* Noualhier 1895 (Reduviidae). Present in southern France and the Mediterranean Iberia, most closely related to *P. katznelsoni* (Dispons 1964) and *P. turkestanica* Putshkov 1984, from Israel and Kazakhstan, respectively (Ribes *et al.*, 1997). They are the only Palaearctic macropterous especies in the genus.

Homoptera

50. *Dudalus javieri* Remane & della Giustina 1997 (Cicadellidae). Known from several steppe areas in the Iberian Peninsula, among them Retuerta de Pina, living on grasses. The other two known species of the genus occur in the Slovak Republic (*D. pallidus* Dlabola 1956) and central Siberia (*D. junatovi* Emeljanov 1964) (Remane & della Giustina, 1997).

Hymenoptera

51. *Psilochalcis frontalis* Askew 1994 (Chalcidoidea, Chalcididae). Known from Monegros, apparently most closely related to *Cephalochalcidia capitata* Nikolskaya 1960 and *C. levis* Nikolskaya 1960, both from Turkmenia (Askew, 1994a). These two species were described from single females, and in Askew (1994a) the differences with *P. frontalis* are discussed. Although described under a separated genus, according to their descriptions differences between these three species seem to be rather tenuous (Askew, 1994a).

52–53. A new species of *Eurytoma* (52) (Chalcidoidea, Eurytomidae) forms galls on *Ephedra nebrodensis* in the Monegros region and Madrid (central Spain) (Askew & Blasco-Zumeta, 1998). In central Asia the Joint Pine is one of the hosts of the only other species of *Eurytoma* known to form galls, *E. flaveola* (Zerova 1976). Although the phyletic relationships of this new species remain uncertain, it is suggested that some morphological similarities with *E. flaveola* may place them in the same species group (Zerova 1976; Askew & Blasco-Zumeta, 1998).

Among the fauna recovered from galls of *E. nebrodensis* in the Monegros there is one species of *Nikanoria*, another genus of eurytomid (53). The two known European species of this genus, which is well represented in the steppes of central Asia (Zerova, 1978), are *N. metallica* (Erdös 1956), from Hungary, Croatia, the former Czechoslovakia, Moldavia, Serbia and central Asia, and *N. ephedrae* (Steffan 1961), from western France. The identity of this species is still uncertain, but it may be *N. ephedrae* (R.R. Askew, unpublished data). It was found in the galls of the new species of *Eurytoma* from Monegros, with no other insect remains, apparently developing as a phytophage inquiline feeding on the vegetable tissue of the gall. Some other species of the genus are reported to be parasitic in cecidomyiid galls (Zerova, 1978), although the biology of the species of *Nikanoria* is still poorly known.

54–55. *Ormyrus monegricus* Askew 1994 (Ormyridae) (54).

So far only known from the Monegros. The species differs considerably from other described species of European *Ormyrus*, and it seems to belong to the same group as *O. oranensis* (Erdös 1964) and *O. ardahanensis* (Doganlar 1991) from Algeria and Turkey, respectively (Askew, 1994b). Some specimens of *O. monegricus* were reared from galls of *Stefaniola salsolae* (Tavares 1904) (Dyptera, Cecidomyiidae), which has an Iberian distribution.

Another new species of *Ormyrus* (55) was found to be a primary ectophagous parasitoid of the larvae of the new species of *Eurytoma* (52) in the Monegros region. It is most closely related to *O. orientalis* Walker 1871 (also present in Monegros), which was described from Sri Lanka, and believed to had spread into western Europe only since the middle of the century (Askew & Blasco-Zumeta, 1998).

56. Among the undescribed fauna of Retuerta de Pina there is a new species of *Ameromicrus* (Chalcidoidea, Torymidae), a genus now considered to be a synonym of *Torymoides* (R.R. Askew, unpublished data). All other species of the former *Ameromicrus* have an eastern distribution, ranging from central Europe (Bulgaria) to Central Asia.

57–58. *Paragymnomerus spiricornis* (Spinola 1808) (57) (Vespoidea, Eumenidae). The nominal subspecies is found in the central Ebro valley, Italy, and the Caucasus (Castro, 1992). A subspecies, *P. spiricornis turanicus* (Kostylev 1940), is found further east in the Turanian region and central Asia.

Ischnogasteroides picteti (Saussure 1852) (58), another eumenid, is found in several localities in Mediterranean Iberia and southern France, and in Turkmenia, Kazakhstan and Mongolia (Castro, 1992). The western populations belong to the nominal form, while the eastern are considered to be a subspecies (*I. picteti tenuis* (Morawitz 1888)).

Lepidoptera

59. *Pachypasa limosa* (de Villiers 1826) (Lasiocampidae) is an Ibero-Magrebbian endemic living on *Juniperus thurifera*. It is most closely related with *P. otus* Dryry, living on *Juniperus* and *Cupressus* species in Asia (Domínguez *et al.*, 1997).

60–61. *Cucullia bubaceki* Kitt 1925 (60) and *C. achilleae* Guenée 1852 (61) (Noctuidae) are Iberian endemics living on *Artemisia herba-alta*, occurring both in the Monegros region (Redondo, 1986 and unpublished data). They are most closely related with *C. argentina* Fabricius and *C. boryphora* Fisher repectively, two Irano-Turanian species (Domínguez *et al.*, 1997).

Psocoptera

62. *Hemineura blascoi* Baz 1994 (Psocoptera, Elipsocidae). So far known only from Monegros. It is most closely related to *H. trudiae* Lienhard & Halperin 1988, from Israel (Baz, 1994).

Thysanoptera

63. A new genus and species of thrip has recently been described with specimens collected over *Krascheninnikovia ceratoides* in the Monegros region, *Blascothrips zumetai* zur Strassen 1997 (Terebrantia, Thripidae). It is so far only known from the type locality (zur Strassen, 1997).

DISCUSSION

The sixty-three species found to have disjunct distributions in la Retuerta and some adjacent habitats, or to form closely related species groups with disjunct distributions, are taxonomically widespread, with examples in ten orders and thirty-seven families (Table 1). With the exception of the Pipunculidae, only one to three species were found in other families of insects, and in the only family of Acari (Table 1). They represent a very low proportion of the wider community, almost negligible in quantitative terms at all levels (species per family and families per order), as noted in the Introduction. This could be expected, as the local persistence of individual species does not exclude the possibility of recent dispersion, or dispersal across geographical barriers, of other species, being the composition of the biota of an area certainly resulting from the interplay of many geographical, ecological and geological factors (Morrone & Crisci, 1995; Andersson, 1996). On a geological scale, species react to climatic changes independently (Huntley & Webb, 1989; Hewitt, 1996; Jablonski & Sepkoski, 1996; Roy *et al.*, 1996), something that contributes to the difficulty of interpreting extant insect assemblages in an historical context. However, this same independence means that the accumulation of examples of a particular pattern in different species and taxa has statistical relevance, and adds to the support for a common explanation.

In evaluating these results it must be remembered that disjunct distributions do not constitute a special biogeographical class on their own (Thorne, 1972). Other species must certainly have the same origin and broad biogeographical relationships. However, because of their persisting widespread distribution, they cannot be separated from species with more recent origin, which dispersed into the Iberian Peninsula during and after the Pleistocene climatic changes. The interest of the disjunct distributions lies in the indirect evidence they provide for evaluating other hypotheses (such the continuous persistence of certain insect species associated with steppe habitats in this case), and the possibility they offer to trace their origin and history — and with them that of the area they inhabit — much more precisely. There is a continuous gradation from common and widespread species, known to occur in almost every suitable habitat within their ranges, and species known to occur only in isolated and very restricted, widely disjunct, populations. As noted in Materials and methods, the cut-off point is in some cases necessarily subjective, and other species with less restricted distributions were not included in the results. This was the case, for example, for *Euodynerus fastidiosus* (Saussure 1853) and *Pseudepipona lativentris* (Saussure 1855), two eumenids with a relatively widespread distribution in Iberia, north-Africa, Sicily, Iran and central Asia, and in Iberia, Corsica, North Africa, Cyprus, Israel, Turkey, the Caucasus, and central Asia, respectively (Castro, 1992). Other examples include Iberian endemic species on typical steppe plants, such as *Oedaspis fissa* Loew 1862 and *Ptiloedaspis tavaresiana* Bezzi 1920 (Diptera, Tephritidae), the latter reared from stems of *Artemisia herba-alba* and the former also swept from the same species (Merz & Blasco-Zumeta, 1995). *Artemisia herba-alba* lives in the steppes of

North Africa east to Israel, and it is considered to have close phytogeographical affinities with *K. ceratoides* (Sáinz-Ollero, Franco Múgica & Arias Torcal, 1996). The closest relative of *O. fissa* seems to be *O. trotteriana* Bezzi 1913, which occurs from Morocco to Israel (B. Merz, unpublished data). Other species not included were those with closest relatives in the central Mediterranean, specially north Africa, such as *Meoneura flabella* Carles-Tolrà 1992 (Diptera, Carnidae), known only from La Retuerta, and closely related to *M. tunisica* Papp 1978, from Tunisia (Carles-Tolrà, 1992).

Similarly, some species have an intermediary distribution between a Mediterranean and a Mediterranean − Turanian range, with known sites as far east as the Caucasus, but not in the main area of the Turanian region (e.g. species 6 and 57). Without a more comprehensive knowledge of the range of each species is not possible to distinguish both types of distributions in detail. Although the distribution of most of the taxa in the north shore of the Mediterranean sea is relatively well known, intermediate populations of some of the species included in this paper are likely to be discovered in the south, specially in North Africa. This could be the case for poorly studied groups, such as the Pipunculidae (De Meyer, 1997). But, as noted above, the existence of small isolated intermediate populations is not a major obstacle in accepting the hypothesis of continuity, specially if found in arid Iberian or North African steppes.

The possible post-Pleistocene origin of the populations of some zooplanktonic eastern species in the saline lagoons of the Monegros region is an example of the risk of interpreting modern disjunct distributions of the same species as a relict of an old wider range (Baltanás *et al.*, 1990). However, though waterfowl are known to be frequent agents for the long dispersal of water invertebrates (and there are recorded recoveries in the Ebro valley of species ringed in eastern Europe and central Asia, Sáez-Royuela & Santos Martínez, 1985; also unpublished data from the Oficina de Anillamiento de la Dirección General de Conservación de la Naturaleza, 1996), this is not the case for their terrestrial counterparts, such as those included in this study. Moreover, the same authors note the existence of an endemic of the same genus of Ostracoda in the Monegros saline lagoons, *Eucypris aragonica* Brehm & Margalef 1948, which does not have known parthenogenetic populations and is as a consequence less able to disperse. This species has an optimum temperature of 2 °C, and it is defined as having a 'cold-stenothermic character' (Santamaría *et al.*, 1992: 96), with a mortality of 50% at only 26 °C, a temperature easily reached in the Monegros (its only know distributional area) for most of the spring and summer. It has also very specific requirements in terms of the ionic composition of the water. A likely explanation seems to be that the species survived the cold arid steppe conditions in the Ebro basin through the Pleistocene, demonstrating the persistence of the same type of saline temporal steppe lakes, with a similar ionic composition and origin– an interpretation reinforced by the existence of disjunct groups of plant species in the same habitat, such as the case of *Microcnemum coralloides* (Loscos & Pardo) Buen (see below). The existence of cold-adapted species

occurring in winter is also known in the North African and central-Asiatic steppes (e.g. Kocher & Reymond, 1954).

The examples of species with their closest relatives in the eastern Mediterranean and/or Turanian and central-Asiatic steppes provide much stronger evidence of the existence of old biogeographical links. In many cases the taxa involved were the only know subspecies of one species (57, 58), or species of one genus or subgenus (36–39, 45, 47, 48, 50, 53, 56). This makes the misinterpretation of close phylogenetic links less likely, which for most of the taxa were based not on cladistic analyses but on the direct interpretation of their morphology. Fully separated insect species are most likely to have a pre-Pleistocene origin (see, e.g. Coope, 1995 or Elias, 1994), although when different subspecies are involved, it is still possible to postulate a more recent, Pleistocene, separation (Hewitt, 1996). In the case of disjunct populations of the same species, no date can be assigned without other information − they may be Holocene in origin, but there are also many known examples of morphological stability of insects for periods over several million years (e.g. Matthews, 1970; Askevold, 1990; − see Elias, 1994 and references therein).

The phytophages which form species complexes with parallel distributional patterns to those of their hosts, and their parasitoids, provide the strongest evidence of the old biogeographical links between the western and eastern steppe faunas. These species usually have a close association with their hosts, and a common origin and a shared history in the same geographical areas is a likely explanation for the common pattern in their phyletic relationships and their distributions.

Among the plant species occurring in Monegros some have west–east disjunct distributions, both across the Mediterranean and in the Turanian region (see Introduction), which support insect species either with disjunct distributions, or which have their closest relatives in the east. *Juniperus thurifera*, the most emblematic plant species of the Monegros region, is known from the North African Atlas, Aragón and other areas in central Spain, with some relict populations in SE France and Corsica. It is most closely related to *J. excelsa* Bieb., from Greece, Anatolia, Middle East, the Caucasus, Iran and Arabia (Barbero *et al.*, 1994). According to the same authors, the Mesogean distribution of both taxa has a Late Tertiary origin. The hypothetic ancestral species had a more northern distribution, the two phyletic lines in both sides of the Mediterranean being ancestor to populations in the Alps to populations in Spain to populations in north Africa for *J. thurifera* in the west, and ancestor to populations of Turkey for *J. excelsa* in the east (Barbero *et al.*, 1994). The SW European populations of *J. thurifera* are thus older, and more similar to the primitive form, than the North African ones, something that excludes a recolonization of the species from North African refugia after or during the Pleistocene.

Krascheninnikovia ceratoides is a member of the Chenopodiaceae distributed in the central-Asiatic steppes, Israel and Sinai in the east, and in the Monegros region (although not in La Retuerta), Alfambra (south Aragón, where it is known by the arab name 'al − arba', Guadix

(Granada, were it seems to be extinct) and Morocco in the west. In the Monegros region it is considered to be a Late Tertiary relict species (Braun-Blanquet & Bolòs, 1957), arrived most probably through north Africa during the Messinien (Sáinz-Ollero *et al.*, 1996). The species has a strong affinity for gypsum soils, and is considered to be typical of the steppes and cold desserts of central Asia (Sáinz-Ollero *et al.*, 1996). The Alfambra and Guadix sites are above 1000 m, but in the Monegros region it is found in the bottom of the valleys — the coldest areas with the less thermophilous flora, due to the frequent thermal inversions in winter (see Material and methods).

Although with a continuous distribution in the Mediterranean and Turanian regions, *Ephedra nebrodensis* (Ephedraceae) is considered here for being host of a number of insects which only occur at both extremes of its distributional range. Several other *Ephedra* species have wide disjunct distributions, something that has been considered a consequence of their very old, Mesozoic, origin (M. Skuhravá, unpublished data).

As seen in the Results, all these plants support both species with disjoint distributions, and species which had their closest relatives in the steppes of the eastern Mediterranean or the Turanian region. This is the case of the complex formed by the species of *Rhagoletis* and *Etsuhoa* with their *Juniperus* hosts (44, 48), an association likely to have a pre-Pleistocene origin, or the species of the genus *Theodorinus* living on *Ephedra* spp. (37). There is another species of weevil living on *E. nebrodensis* in the Monegros, *Paroxyonyx imitator* (Wagner 1928). The species was described from Albarracín (province of Teruel, S Aragón), and it is considered to be an Iberian endemic (Colonnelli, 1995). According to the same author, the group of genera of Ceutorrhynchinae living on *Ephedra* form a monophyletic group strongly linked with their host species, and with many morphological modifications considered to be an adaptation to their host plants.

The incomplete knowledge of the distribution of some groups makes difficult the interpretation of apparent endemics, such as the genus *Blascothrips* (63), living on *Krascheninnikovia ceratoides* in Monegros, or *Albarracina warioniz* (Oberthür 1881) (Lepidoptera, Lymantridae), an Ibero-Maggrebian endemic living on *Ephedra* spp. There is a complex community of phytophages, parasitoids and hyperparasitoids living on the galls and seeds of *Ephedra nebrodensis* in Monegros, including a new genus and several undescribed species (Askew & Blasco-Zumeta, 1997, 1998). Rather than their still uncertain phyletic relationships, what is most relevant is the fact that most of them are apparently endemic species with intricate trophic relationships. Although it is likely that there are other gallicolous hosts on *Ephedra*, these complex relationships are clearly an additional support to the evidence of the old presence of the hosts in the area. It would be most interesting to know if the same (or other) species of these groups occur over the same plant in their eastern realm or in north Africa.

In addition to the species mentioned above, the only extant woody Cruciferae in Europe are the Ibero-Mauritanic endemic species of the genus *Vella*, which are though to be relicts from the Late Miocenic steppes. One of them, *V.*

pseudocytisus L. is found in central and southern Spain and in Morocco, with a subspecies endemic to the central Ebro valley and southern Aragón (Gómez-Campo, 1981; Castroviejo, 1993). Woody species of Cruciferae are common in central Asia, the supposed centre of origin of their western relatives (Gómez-Campo, 1981; Domínguez *et al.*, 1996). *Microcnemum coralloides coralloides* (Salicorniaceae), described from the Monegros region, is found in Mediterranean Iberia, on saline soils over Miocenic deposits. It has one subspecies, *M. coralloides anatolicum* Wagenitz 1959, distributed through central Turkey and Syria, also on saline soils (Molero, 1986). There are also some examples of disjunct distributions among the lichens found in Retuerta de Pina, such as *Psora saviczii* (Tomin) Follm. & Crespo, found in several arid steeps in Spain, Ukraine and Kazakhstan (Barreno, 1991 and J. Etayo, unpublished data), or *Teloschistes lacunosus* (Rupr.) Sav. and *Diploschistes diacapsis* (Ach.) Lumbsch. (= *steppicus*), steppe species distributed in the central Ebro valley, the Negev desert, and areas with gypsum soils in Crimea and other Caspian republics, a pattern found among several Mediterranean — Turanian gypsiferous species (Llimona, 1973; Egea & Alonso, 1996; J. Etayo, unpublished data). There are other numerous examples of biogeographical links between the flora of NW Africa (some species extending their distribution to the Iberian Peninsula) with SW and central Asia, and the favoured explanation is that present populations (of the same or related vicariant species) are the remnants of former continuous distributions across the central and southern Palaearctic region during most of the Late Tertiary (Davis & Hedge, 1971). In some cases there is direct fossil evidence of the survival of species previously considered to be of recent origin, such as the walnut (Carrión & Sánchez-Gómez, 1992). The immediate response of some trees to local amelioration after full glacial periods in south Spain provides also direct evidence of their persistence in nearby refugia (e.g. *Quercus ilex*-type forest in Padul, Granada, Pons & Reille, 1988). In other cases, as seen above with the *J. thurifera — J. excelsa* complex, their phylogeneic reconstruction demonstrates an older origin for the SW European populations, excluding the possibility of a recent re-colonization from North Africa. The existence of a numerous Ibero-Maggrebian endemic fauna on *J. thurifera* is an additional support to this hypothesis, such as the Lepidoptera Geometridae *Afriberina tenietaria* (Staudinger 1900), *Ecleora solieraria* (Rambur 1834), and *Menophra thuriferaria* (Zerny 1927), all living in Retuerta de Pina (Domínguez *et al.*, 1997; V.M. Redondo unpublished data). The response to climatic changes could have been for some species a regional displacement in altitude, or the tracking of ecological refugia in heterogeneous landscapes, in contrast to latitudinal or longitudinal changes of much broader scope (Hewitt, 1996; Huntley, 1996; see, e.g. Noonan, 1990 for an example with ground beetles of the Chihuahuan desert).

In the case of the species occurring in steppe areas over gypsum soils there is the possibility of a strong link between their distribution and that of the gypsiferous soils themselves. Although of a varied origin and age, most of the areas with extensive gypsiferous soils in the western

Palaearctic predate the Pleistocene, and share an arid climate and a steppe or open woodland vegetation (Alphen & Ríos Rómero, 1971, see Fig. 1). Gypsiferous soils harbour a very particular flora (see, e.g. Llimona, 1973; or Guerra *et al.*, 1995; for lichens), and the strong correlation between their age and the number of endemics living on them has been demonstrated for habitats in the Nearctic region (Turner & Powell, 1979). Although the detailed distribution and biology of most of the species included in this paper is still poorly known, the study of their relationships with gypsum soils and their associated flora is likely to be of great relevance for the understanding of the origin of their disjunct distributions.

There is also evidence of the persistence in the Monegros region of lineages reflecting distributional patterns older than those studied in this paper. Thus, the only living Palaearctic species of Myrmecolacidae, a family of Strepsiptera distributed over the circum-tropical regions, are *Lychnocolax hispanicus* Kathirithamby & Kifune 1991, so far only known from La Retuerta, and *L. lundensis* Luna de Carvalho 1956, described from Angola (Luna de Carvalho, 1956) and with only one known Palaearctic population, also in La Retuerta (J. Kathiritamby, unpublished data). There is one fossil species, *Stichotrema eocaenicum* (Haupt), from the Eocene brown coal in Germany, a time with a tropical climate (Hallam, 1994). In the northern Hemipshere, the only living Nearctic species is a recent introduction, brought from the Neotropics with tropical ants (Kathirithamby & Kifune, 1991). Although the biology of the two species of Myrmecolacidae from Monegros is totally unknown, males of this family usually have a very short adult life (no more than 12 h), and are known to be parasitoids of ants. Of the forty-nine species of ants found in La Retuerta, only one is cosmopolitan (*Hypoponera eduardi* (Forel 1894)), and several are Iberian or Ibero-provenzal endemics (eleven, one of them an endemic species described from La Retuerta, Espadaler, 1997). The females are also endoparasitic and apterous. It is unlikely that both species of Myrmecolacidae were recent introductions from sub-Saharan Africa.

CONCLUSIONS

This paper necessarily has a preliminary character. The detailed study of the phylogeny of the species discussed, as well as that of the high number of new species the relationships of which are totally unknown, will undoubtedly contribute to the resolution of the many questions which remain unanswered. Similarly, increased knowledge of the detailed distribution of the many new species described from La Retuerta will allow a better understanding of the biogeography of the wider community.

Meanwhile, although the only direct means to demonstrate conclusively the persistence of insect populations in steppe environments in the Monegros region through the Pleistocene would probably be the study of the genetic variability across their whole range, the accumulated evidence of the same biogeographical patterns in a broad array of taxonomic groups is, in our opinion, strong evidence favouring the hypothesis of their former continuity. It is always possible to found alternative *ad hoc* historical justifications for the distribution of individual species, but the accumulation of examples calls for a more parsimonious common explanation (a common biogeographical track in the sense of Croizat, 1958), which is likely to be strongly related to the distribution of gypsiferous soils of Miocene origin. On the other hand, the biogeographical links demonstrated by the disjunct distribution of closely related species cannot be discarded on the basis of the possibility of trans-Palaearctic Pleistocene shifts in their ranges, because one major consequence of these shifts is the evolutionary stability of such species due to frequent genetic mixing (Coope, 1979, 1995).

The increasing body of evidence supporting the persistence of both plant communities and climatic and landscape regional characteristics in the arid areas of the central Ebro valley is also a contributing factor to accepting the conclusion of a parallel persistence of at least some steppe insect species, which can be considered relicts of a widespread Late Tertiary trans-Palaearctic fauna, the remnants of which have in the Monegros region the best known example in the Iberian Peninsula.

Unfortunately, the continuity of the steppe habitats in the Monegros region is now far from guaranteed. The agricultural plans for the area include the development of an intensive irrigation scheme, with the disappearance of at least all major saline lagoons and surrounding habitats (and with them endemics such as *Eucypris aragonica*). A proposal for the designation of a Natural Park including some areas within the Monegros region has recently been rejected by the autonomous goverment of Aragón. The Late Tertiary landscape of the Monegros, with the plant and insect populations which were the basis for the description of more than one hundred new species to science, are clearly at risk − and with them the possible answer to key questions on the biogeography of south-western Europe.

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