

# Biogeography of bees (Hymenoptera, Apoidea) in Sahara and the Arabian deserts

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We discuss the distribution ranges of 57 species of bees (representing 19 genera and 7 sub-families) within a region including the Sahara and Arabian deserts and their adjacent areas (SAD). More than 8,000 biogeographical records for a total of 291 species of bees were included in this study. We calculated several biodiversity indices and show that the study area is characterised by high species diversity (33%) and endemism (58%) rates. Our results show that composition of the SAD fauna results mainly from a “Nearest Neighbour Effect”, implying the adjacent areas. However, the influences of more distant areas, like Central Asia and the sub-Saharan region, are also significant, notably in their contribution to species endemism. The comparison of the distributions of the studied species support the description of diversity hotspots in specific areas: western Atlas (Morocco), eastern Atlas (Tunisia), Tripolitania, Cyrenaica, Nile Valley, Jordan Valley and Oman hills. Five distributional patterns, fitting the ranges of the studied species, are described. The local water availability and the historical cycles of ecological changes in SAD are hypothesised powerful explanatory factors of the observed distributions shapes.

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## Introduction

The Apoidea s.str. (commonly known as bees) constitute a group of more than 16,000 species throughout the World (Michener 2000). Bees are present in most ecosystems, where they are primarily responsible for the pollination of flowering plants, playing a key-role in ecosystems dynamics. An outline of the distribution of bees worldwide is available in previous works (Michener 1979, 2000; Radchenko & Pesenko 1994; Roubik 1989), which underline basically the link between bee diversity and xeric climate (Michener 1979, 2000). Generally, bees are more abundant and diverse in the warm temperate xeric ecosystems, e.g., the Mediterranean Basin, southwestern Nearctic and southern Africa (Eardley 1996; Kuhlmann 2005; Moldenke & Neff 1974; Rasmont et al. 1995).

These conclusions have been used to discuss various aspects of the evolution of bees, notably the age of the divergence between sphecid-wasps and bees and the Gondwanian geographical origin of the group. A few recent works have brought support to these conclusions or suggested alternative hypotheses (Danforth et al. 2004; Danforth & Ascher 1999; Leys et al. 2000, 2002).

In contrast, only few studies have been dedicated to more accurate descriptions of bee distribution and diversity within their areas of higher abundance. At the local scale, it has been repeatedly demonstrated that bees usually follow “patchy” distributions, according to resource availability (Cane et al. 2005; Kuhlmann 2005; Mayer & Kuhlmann 2004; Minckley et al. 2000; Sipes & Wolf 2001). However, these studies have not led to

broader biogeographic conclusions. The interrelationships between populations in regional and sub-regional scales remain in most cases elusive. However, answers to such questions are essential for understanding biogeography in the evolution of bees.

In the present study, we investigate the biogeography of seven recently reviewed subfamilies of wild bees with representatives in the Saharan and Arabian deserts and neighbouring areas. The main goals of the present study are: 1. to estimate bee diversity and endemism rates; 2. to define the biogeographical relationships with adjacent bee faunas (Western Palaearctic, Eastern Palaearctic and sub-Saharan); 3. to identify and describe the regional distributional patterns; 4. to define limiting factors that might confine species ranges.

## Material and Methods

### *Geographical framework*

The study abbreviated (abbreviated hereafter as SAD = Sahara + Arabian Desert) is centred on the two deserts occupying the southern part of the Western Palaearctic: the Sahara and Arabian deserts. It is limited northward by the Mediterranean Sea and the southern Turkish border (roughly 35°N), eastward, by the Iranian border and the Persian Gulf, southward by the parallel of N'Djamena (Chad), and westward by the Atlantic (Fig. 1).

As a corollary of the ecological optimum of the studied species, the present paper focuses mainly, within SAD, on the Mediterranean-like ecosystems of the studied framework. In addition to fit to the bees' ecological optimum, SAD displays other interesting geomorphological features. Most ecosystems expand subparallel to latitudes (Adams & Faure 1997; White 1986; Olago 2001; NGS 2001; Zohary 1973), as well as the main mountain chains. It can be hypothesised that both have analogous effect on bee dispersal.

### *Bioclimatological sketch of the study territory*

Relationships between bioclimatological features and local species richness of various groups of organisms have been demonstrated (Andrews & O'Brien 2000; Ceballos & Brown 1995). Such studies have not yet been produced for bees. However, based on the available works (Michener 1979, 2000; Radchenko & Pesenko 1994; Roubik 1989) it can be assumed that these ecological parameters are of main importance for the dispersal of bees also.

The knowledge of the bioclimatic features and eco-climatic history of SAD has been notably improved in the last three decades (Adams & Faure 1997; Olago 2001; NGS 2001; White 1986; Zohary 1973). In northern Africa and the Arabian Peninsula, the core tropical desert formations are surrounded by concentrically arranged zones of

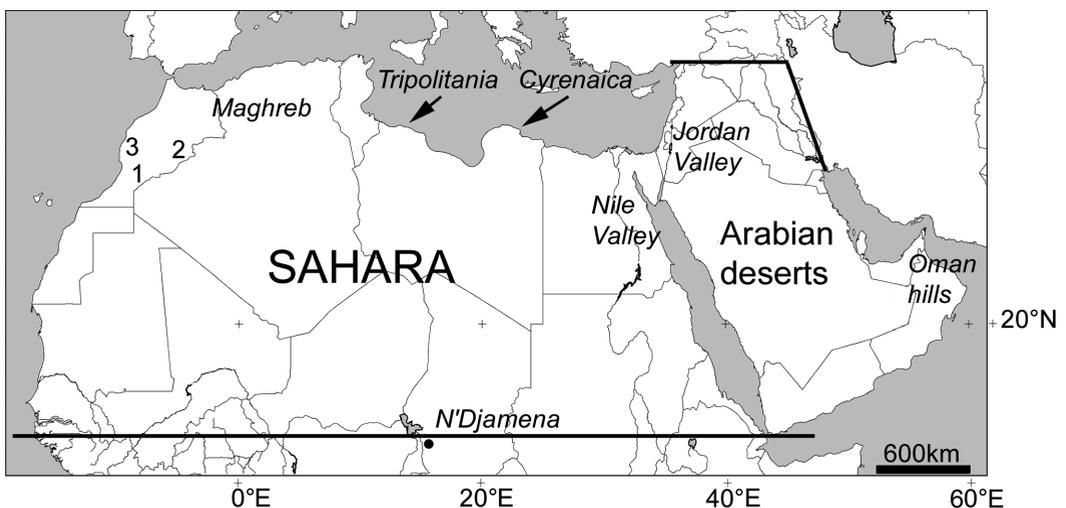


Fig. 1. Study area and particular region (1=Drâa Valley; 2=Ziz Valley; 3=Souss Valley).

vegetation types requiring moister climates (Adams & Faure 1997; Olago 2001; NGS 2001). Within these zones, mountains play an important role in creating regional climatic and ecological clines. One good example is found in the Atlas mountains, which constitute an extended transition gradient between Mediterranean and Saharan environments. In addition to these mountain chains, the isolated massifs dotting the whole SAD (e.g., Ennedi, Hoggar, Tibesti) also constitute areas of local bioclimatic and ecological gradients (Olago 2001; White 1986).

Like the northern West-Palaearctic, SAD has undergone several cycles of severe climate changes during Tertiary and Quaternary (i.e., encompassing the time range of modern bees). These cycles can be roughly summarized as alternating episodes of dry and moist conditions, as observed during the glacial cycles in the Quaternary. The present bioclimatological condition can be considered as a dry episode close to the conditions during the previous glacial maxima (Adams & Faure 1997; Marchant & Hooghiemstra 2004). The deserts are currently expanding substantially, approaching their known maximal extent, while the moister Mediterranean, Pre-Saharan and Sahelian ecosystems are restricted to discontinuous surrounding belts. This episode started approx. 5.000 years BP and was preceded by a moist, greening phase. During this latter, the deserts were substantially smaller than at present, whereas the surrounding steppe-like ecosystems (Mediterranean and Pre-Saharan) were much larger and continuous (Adams & Faure 1997; Marchant & Hooghiemstra 2004), favouring dispersal of the organisms associated with them.

#### Study taxa

The present study targets seven bee subfamilies, selected for the availability of the biogeographical records and the accuracy of the current systematic knowledge: Dasypodainae (Melittidae), Fideliinae (Megachilidae), Lithurginae (Megachilidae), Meganomiinae (Melittidae), Melittinae (Melittidae), Panurginae (Andrenidae) and Rophitinae (Halictidae). *Dufourea* is not considered because of shortage of available biogeographical information. The distributions and diversity of these taxa are given in Table 1. In total, 19 genera and 291 species were included. The distributions of the 57

species endemic to SAD are summarised in Table 2 and discussed hereafter.

For higher level systematics, we refer to Michener (2000). At the generic and specific levels more recent works were used as taxonomic references: Michez et al. (2004a, b) for *Dasypoda* Latreille; Michez & Patiny (2005) for *Macropis* Panzer; Patiny (2001, 2004b) for all genera in Panurginae; Patiny & Michez (2006) for *Systropha* Illiger. These sources for species taxonomy insure the homogeneity in the treatment of the species and genus concepts.

The biogeographical data were acquired from both collections and published literature. The following references were consulted: Engel (2002), Warncke (1979, 1980), Whitehead & Eardley (2003) for Fideliinae; Eardley (1988), Van Der Zanden (1987) for Lithurginae; Warncke (1973), Michener (1981), Michez et al. (2004a,b, 2007), Michez (2005), Michez & Patiny (2005) and Pauly et al. (2001) for Melittidae; Baker (1972), Patiny (2001, 2004a,b), Warncke (1972, 1985, 1987) for Panurginae; Baker (1996), Eardley (1991b), Ebmer & Schwammberger (1986), Patiny & Michez (2006), Schwammberger (1975) for Rophitinae. The biogeographical records are digitised in the BDFGM (*Banque de Données Fauniques Gemblox-Mons*: <http://www.zoologie.umh.ac.be/hymenoptera>). The distribution files were produced using the software package DFF-CFF (Barbier & Rasmont 2000; Barbier et al. 2000).

#### Diversity and endemism indices

We used three indices (D, O, R), computed for each genus separately, to describe the SAD fauna (Table 1). O and R are derived from other indices used in similar studies (Emberton et al. 1997).

The taxonomic diversity in the study area was calculated for each genus using the original D index:

$$D = (SN/T)*100$$

SN is the number of species of each genus in the study area; T is the total number of species included in the genus.

The originality of the regional fauna was evaluated using the O index:

$$O = (ESN/T)*100$$

ESN is the number of species of each genus endemic to SAD; T is the total number of species included in the genus.

**Table 1.** Generic distribution and species diversity of the seven subfamilies of wild bees included in this study. The total number of genera in each taxon is indicated in parentheses (first) and the number of genera in the Eastern Hemisphere is given after the hyphen. **T**, (total) number of described species; **EU**, number of species in Europe; **EP**, number of species in Eastern Palearctic region (including Central Asia); **S**, number of species in sub-Saharan region; **NA**, number of endemic species in north-Africa; **AP**, number of endemic species in the Arabian Peninsula; **SN**, number of species in Sahara and Arabian deserts; **ESN**, number of endemic species in study territory; **D**, diversity index ( $=(\text{SN}/\text{T}) * 100$ ); **O**, originality index ( $=(\text{ESN}/\text{T}) * 100$ ); **R**, endemism index ( $=(\text{ESN}/\text{SN}) * 100$ ). D, O and R values are boldfaced when under 20%.

| Taxa                                  | Generic distribution   | T   | EU  | EP | S  | NA | AP | SN | ESN | D %       | O %       | R %      |
|---------------------------------------|------------------------|-----|-----|----|----|----|----|----|-----|-----------|-----------|----------|
| <b>Dasypodainae (6-6)</b>             |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Dasypoda</i>                       | Palearctic             | 33  | 20  | 5  | 0  | 3  | 4  | 15 | 8   | 45        | 24        | 53       |
| <i>Promelitta</i>                     | north African          | 1   | 0   | 0  | 0  | 1  | 0  | 1  | 1   | 100       | 100       | 100      |
| <b>Fideliinae (3-2)</b>               |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Fidelia</i>                        | sub-Saharan            | 7   | 0   | 0  | 6  | 1  | 0  | 1  | 1   | <b>14</b> | <b>14</b> | 100      |
| <i>Pararhophites</i>                  | Palearctic             | 3   | 1   | 2  | 0  | 1  | 0  | 1  | 1   | 33        | 33        | 100      |
| <b>Lithurgini (3-1)</b>               |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Lithurgus</i>                      | World                  | 26  | 4   | 4  | 4  | 5  | 3  | 5  | 1   | <b>19</b> | <b>4</b>  | 20       |
| <b>Melittinae (4-4)</b>               |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Macropis</i>                       | Holarctic              | 16  | 3   | 9  | 0  | 2  | 0  | 2  | 0   | <b>13</b> | <b>0</b>  | <b>0</b> |
| <i>Melitta</i>                        | Old World and Nearctic | 44  | 15  | 18 | 5  | 3  | 3  | 3  | 2   | <b>7</b>  | <b>5</b>  | 66       |
| <b>Meganomiinae (4-4)</b>             |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Meganomia</i>                      | sub-Saharan            | 5   | 0   | 0  | 4  | 0  | 1  | 1  | 1   | 20        | 20        | 100      |
| <i>Uromonia</i>                       | sub-Saharan            | 2   | 0   | 0  | 2  | 1  | 0  | 1  | 0   | 50        | <b>0</b>  | <b>0</b> |
| <b>Panurginae (34-14)</b>             |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Avpanurgus</i>                     | SAD                    | 1   | 0   | 0  | 0  | 1  | 0  | 1  | 1   | 100       | 100       | 100      |
| <i>Borgatmelissa</i>                  | SAD                    | 2   | 0   | 0  | 0  | 0  | 2  | 2  | 2   | 100       | 100       | 100      |
| <i>Camptopoeum</i>                    | Palearctic             | 29  | 10  | 16 | 0  | 5  | 7  | 11 | 6   | 38        | 21        | 55       |
| <i>Clavipanurgus</i>                  | Palearctic             | 12  | 9   | 2  | 0  | 1  | 4  | 5  | 2   | 41        | <b>17</b> | 40       |
| <i>Melitturga</i>                     | Old World              | 15  | 7   | 2  | 5  | 4  | 4  | 8  | 3   | 53        | 20        | 38       |
| <i>Melitturgula</i>                   | Old World              | 12  | 0   | 0  | 9  | 2  | 3  | 4  | 3   | 33        | 25        | 75       |
| <i>Panurgus</i>                       | Palearctic             | 34  | 13  | 2  | 0  | 23 | 6  | 25 | 18  | 74        | 53        | 72       |
| <i>Plesiopanurgus</i>                 | Palearctic             | 4   | 2   | 2  | 0  | 1  | 0  | 1  | 1   | 25        | 25        | 100      |
| <b>Rophitinae (13-5)</b>              |                        |     |     |    |    |    |    |    |     |           |           |          |
| <i>Rhophites</i>                      | Old World              | 19  | 14  | 6  | 0  | 1  | 2  | 3  | 1   | <b>16</b> | <b>5</b>  | 33       |
| <i>Systropha</i>                      | Old World              | 26  | 2   | 9  | 7  | 3  | 6  | 6  | 5   | 23        | <b>19</b> | 83       |
| <b>Sums – D, O, R for all species</b> |                        | 291 | 100 | 77 | 42 | 58 | 45 | 96 | 57  | 33        | <b>19</b> | 58       |

The degree of endemism was evaluated using the R index.

$$R = (\text{ESN}/\text{SN}) * 100$$

ESN is the number of species endemic in SAD; SN is the total number of species of the genus in the study area.

## Results

### 1. Diversity, endemism rate and originality

The seven studied subfamilies contain 67 genera, of which 36 are present in the Eastern Hemisphere (Michener 2000). Nineteen of them (53%), are found in SAD but only three (*Avpanurgus*, *Borga-*

*tomelissa* and *Promelitta*) are endemic (Table 1). The other 16 occur, at least partly, in the adjacent areas. The originality and endemism indices (O, R), calculated in generic rank, are consequently low, reaching respectively 4% and 16%.

The same indices calculated for all the species in SAD are notably high. The taxonomic diversity (D) is lower (33%) than for genera, but originality (19%) and endemism (58%) are significantly higher (Table 1). Even when displaying a low diversity, genera are characterised by a high rate of species endemism. This is particularly obvious for *Rophites* and *Melitta*, which have rather low diversity in SAD (under 20%) but display a high endemism rate (equal to higher than 33%). Strong variation in these indices is observed among the studied taxa. For instance, the Melittinae have notably low diversity rates, while Panurginae and Dasypodainae display higher scores.

2. Biogeographical relationships

Close biogeographical relationships between the Western Palaearctic (Northern Mediterranean Basin) and SAD faunas are clearly underlined by the previous results, notably through the low level of generic endemism. Together with the known phylogenetic relationships of the studied taxa, these results can also be used to describe more accurately the biogeographical relationships of the SAD and the adjacent regions.

What we call hereafter the nearest neighbour effect (NNE) can be exemplified by the distribution ranges of taxa such as *Panurgus* (*Pachycephalopanurgus*). In *Panurgus*, the subgenus *P.* (*Pachycephalopanurgus*) constitutes a robust monophyletic group (Patiny 1999a, 2001), with maximum diversity in the Maghreb (as defined in the present paper, the Mediterranean and Atlantic seaboard and adjacent mountain ranges north of the Sahara of Morocco, Algeria, and Tunisia) (Patiny & Gaspar 2000b; Patiny et al. 2005) (Fig. 2). The species included in this subgenus are either endemic to the Maghreb (*Panurgus convergens*, *Panurgus rungsii*), occur in adjacent areas (*Panurgus canescens*, *Panurgus meridionalis*), or display a wider distribution with many local populations in SAD (*Panurgus nigriscopus*) (Fig. 2). *P. meridionalis* and *P. canescens* are actually the only species of *Pachycephalopanurgus* absent from SAD. The core populations of *P.* (*Pachycephalopanurgus*) are thus typically ranging in SAD and the species absent are present in adjacent areas. A simple hypothesis invoking recent dispersal can be inferred between close neighbours (NNE). According to the maps published in Michez et al. (2004b), other putative examples of the NNE can be found in *Dasypoda*.

In contrast, *Plesiopanurgus zizus*, *Pararhophites quadratus* and *Clavipanurgus desertus* belong to genera that are almost absent from SAD and whose core range is located in eastern Turkey or

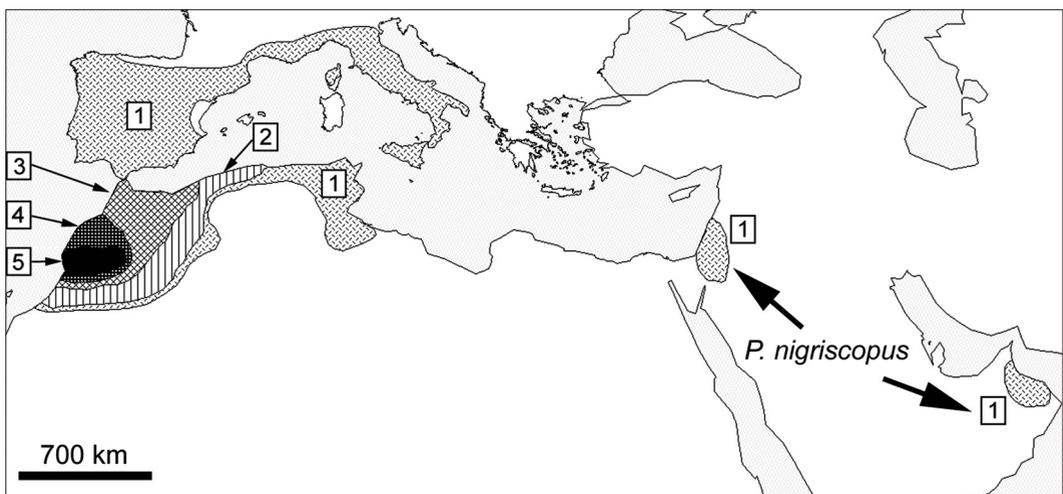


Fig. 2. Isodiversity curves in *Panurgus* (*Pachycephalopanurgus*) based on the known distributions of the included species. Numbers and greyscales areas figure the diversity gradients in the subgenus distribution (1=one species).

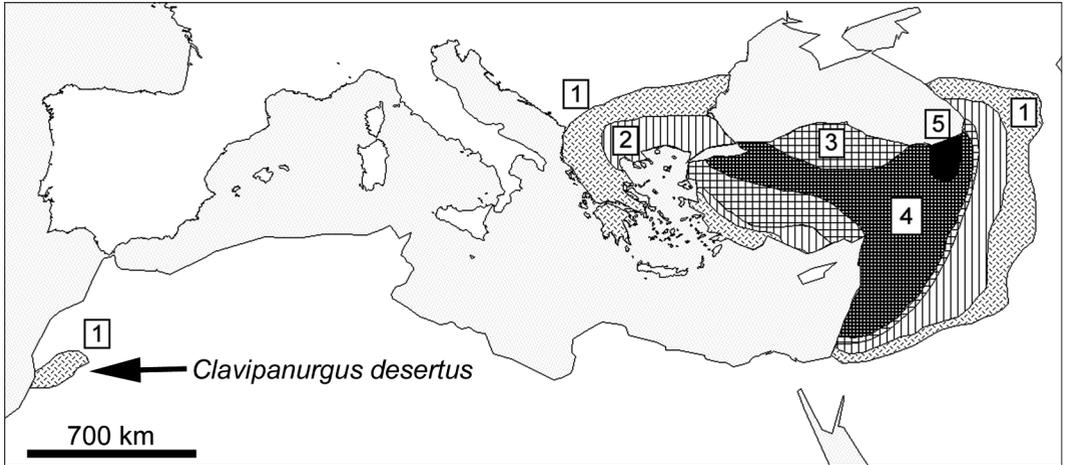


Fig. 3. Isodiversity curves in *Clavipanurgus* based on the known distributions of the included species. Numbers and greyscales areas figure a diversity gradient in the genus distribution (1=one species).

Central Asia (Patiny 2001, 2003; Patiny & Rasmont, 1999; Schwammbeger, 1971; Warncke 1979). Distributions of these taxa include wide disjunctions between the isolated species in SAD and the remaining eastern species. Nearly all of the 12 species of *Clavipanurgus* were recorded

from Turkey and Caucasus, except *Clavipanurgus gusenleitneri*, which occurs in Syria, close to the core distribution, and *Clavipanurgus desertus*, which occurs in Morocco and is endemic in SAD (Fig. 3). Likewise, in *Pararhophites* two of the three described species are restricted to Iran, Ka-

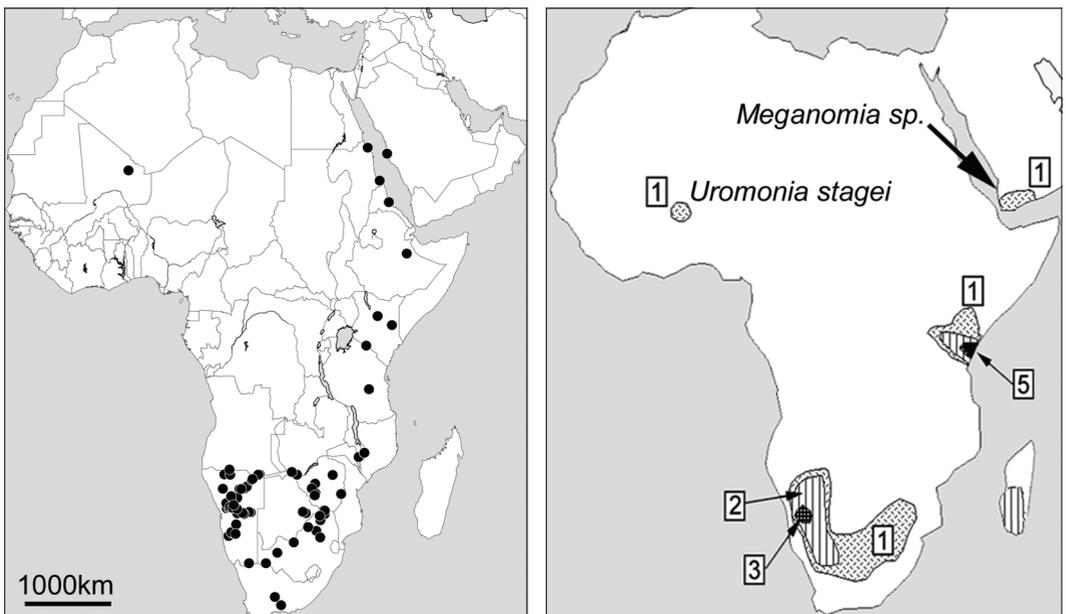


Fig. 4. a. Distribution of *M. scriptifrons*. b. Isodiversity curves figured in Meganomiinae based on known distributions of the included species. Numbers and greyscales areas figure the diversity gradients in the subfamily distribution (1=one species).

zakhstan, Pakistan, Uzbekistan and Turkmenistan. *Pararhophites quadratus* is the only species occurring in SAD, where it is endemic and isolated). In *Plesiopanurgus*, only *Plesiopanurgus zizus* is endemic to Morocco, the other three species occur in Iran, Turkey and Pakistan. In these three examples, the distributions of genera are largely disjunct and the NNE does obviously not satisfyingly explain the present distribution.

The biogeographical relationships between the sub-Saharan and SAD faunas also display examples of disjunct distributions. The presence in SAD of species such as *Lithurgus pullatus*, *Meliturgula scriptifrons*, *Uromonia stagei* and *Melitturga albescens* demonstrate the existence of biogeographical relationships between SAD and Subsaharan Africa (Figs 4a, b). *L. pullatus* and *M. scriptifrons* are very widely distributed in the sub-Saharan region (Eardley 1988; Patiny 1999b; Patiny & Gaspar 2000a). The populations of these two species recorded in northern Egypt (*L. pullatus*), in Saudi Arabia (*M. scriptifrons*) and in western Africa (*M. scriptifrons* in Tilemsi Valley, NE Mali) can be regarded as the northernmost representatives of more widely distributed taxa. *Uromonia stagei* is rare in Africa. The genus is represented by *Uromonia flavitarsis* in Madagascar and *Uromonia stagei* in Kenya. Within SAD, *U. stagei* has been recorded in the Niger Valley (northern Mali) (Figs 4a, b).

Likewise, *Melitturga (Australomelitturga)* is the only subgenus of *Melitturga* to be present in

southern Africa (Patiny 1999a, 2001; Patiny & Gaspar 2000a). Four of the five described species are found in this region (Angola, Namibia, South Africa). *M. albescens* is the only Palearctic species (Atlas Mountains and Tafilalet in Morocco, Hoggar in S. Algeria and in Tunisia).

These distribution of predominantly Central Asian and southern African taxa in SAD include large disjunctions between the core populations and the isolates in SAD. Such disjunctions cannot be satisfyingly explained by a NNE. They could possibly be relictual, reflecting much wider ancestral distributions that have been fragmented by climatic (see above: bioclimatological sketch) or geological events.

### 3. Biodiversity hotspots and distributional patterns

The comparison of the distributions of the studied species underlines the existence of local diversity hotspots in western Atlas (Morocco), eastern Atlas (Tunisia), Tripolitania (Libya), Cyrenaica (Libya), Nile Valley, Jordan Valley and Oman hills (Figs 1, 5). The five distributional patterns described here consist of similarly repeated combinations of these spots within the distributions of various species.

*Multilocular distributions.* – Among the studied taxa, 10 species occur through the whole study area displaying what we call a “multilocular distributional pattern” (Table 2). The range of *Panurgus*

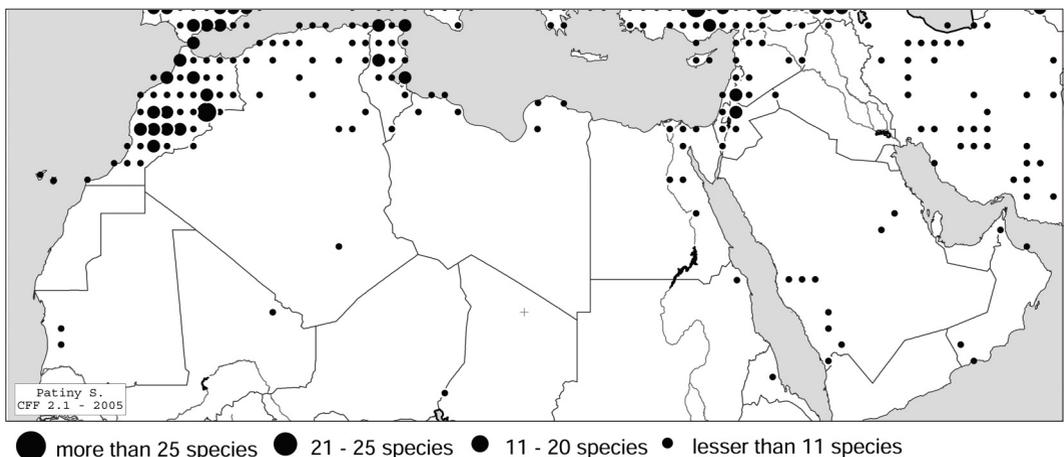


Fig. 5. Species diversity in the study area in 1° squares. The most diversified of these areas (larger dots) constitute the hereafter discussed distributional spots.

**Table 2.** Species endemic in SAD and their distributional patterns (1 = Multilocular; 2 = Mauritanian; 3 = Arabian; 4 = Sahelian; 5 = Local). Distributions are given using FIPS alphabetical roots; the acronyms are: AG, Algeria; DJ, Djibouti; EG, Egypt; ET, Ethiopia; IS, Israel; JO, Jordan; LY, Libya; MO, Morocco; MR, Mauritania; MU, Oman; NI, Niger; QA, Qatar; SA, Saudi Arabia; SN, Senegal; SP, Spain; SY, Syria; TC, United Arab Emirates; TS, Tunisia; YE, Yemen.

| Taxa   | Distribution               | Pattern           | Taxa                                    | Distribution           | Pattern        |
|--|----------------------------|-------------------|---|------------------------|----------------|
| <b>Dasyopodinae</b>                              |                            |                   |   |                        |                |
| <i>Dasyopoda albipila</i> Spinola 1838           | IS, MU, QA, SA             | 3                 | <i>Melitturga albescens</i> Pérez, 1895 | AG, MO, TS             | 2              |
| <i>D. brevicornis</i> Pérez 1895                 | AG, TS                     | 2-NE Africa       | <i>M. krausi</i> Schwarz 2003           | IS                     | 5-Israel       |
| <i>D. gusenleitneri</i> Michez 2004              | JO                         | 5-Jordan          | <i>M. orantensis</i> Lepeletier 1841    | AG, EG, MO, TS         | 1              |
| <i>D. maura</i> Pérez 1895                       | AG, MO                     | 2-NW Africa       | <i>Melitturgula denesia</i> Patiny 1999 | JO                     | 5-Jordan       |
| <i>D. orantensis</i> Pérez 1895                  | AG, MO                     | 2-NW Africa       | <i>M. ornata</i> (Popov 1951)           | SA                     | 5              |
| <i>D. sinuata</i> Pérez 1895                     | AG, EG, LY, MO, SP, TS     | 1                 | <i>M. senegaliae</i> Patiny 1999        | SN                     | 5-Senegal      |
| <i>D. syriensis</i> Michez 2004                  | SY                         | 5-Syria           | <i>Panurgus acutus</i> Patiny 2002      | MO                     | 5-Argan region |
| <i>D. toroki</i> Michez 2004                     | IS                         | 5-Israel          | <i>P. avarus</i> Warncke 1972           | AG, MO                 | 2              |
| <i>Promelitta alboclypeata</i> (Friese 1990)     | EG, MO                     | 4                 | <i>P. calceatus</i> Pérez 1895          | AG, MO, TS             | 2              |
| <b>Fidelinae</b>                                 |                            |                   |   |                        |                |
| <i>Fidelia ulrikei</i> Warncke 1980              | MO                         | 5-S. Morocco      | <i>P. convergens</i> Pérez 1895         | AG, MO                 | 2              |
| <i>Pararhopites quadratus</i> (Friese 1898)      | EG, MO, TS                 | 1                 | <i>P. cyrenaikensis</i> Warncke 1972    | LY                     | 5-Libya        |
| <b>Lithurgini</b>                                |                            |                   |   |                        |                |
| <i>Lithurgus cephalotes</i> Van Der Zanden 1977  | MO                         | 5-W. Morocco      | <i>P. dentatus</i> Friese 1901          | IS, JO, LY, MO, SA, TS | 1              |
| <b>Meganomiinae</b>                              |                            |                   |   |                        |                |
| <i>Meganomia</i> sp. (undescribed species)       | YE                         | 5-Yemen           | <i>P. farinosus</i> Warncke 1972        | AG, MO                 | 2              |
| <b>Melittinae</b>                                |                            |                   |   |                        |                |
| <i>Melitta aegyptiaca</i> Radoszkowski 1891      | EG, IS, MO, SP             | 1                 | <i>P. maroccanus</i> Pérez 1895         | AG, MO                 | 2              |
| <i>M. schmiddecknechti</i> Friese 1898           | AG, EG, IS, LY, MO, SP, TS | 1                 | <i>P. minor</i> Warncke 1972            | MO                     | 5-Argan region |
| <b>Panurginae</b>                                |                            |                   |   |                        |                |
| <i>Avpanurgus flavofasciatus</i> (Warncke 1972)  | AG                         | 5-Algeria         | <i>P. nigricapillus</i> Pérez 1895      | AG, IS, MO, MU         | 1              |
| <i>Boragatomelissa brevipennis</i> (Walker 1871) | DJ, ET, NI, SA, MR         | 4                 | <i>P. niloticus</i> Warncke 1972        | AG, MO                 | 2              |
| <i>B. niveopilosa</i> Patiny 2002                | SA                         | 5-Saudi Arabia    | <i>P. ovatulus</i> Warncke, 1972        | MO                     | 5-Morocco      |
| <i>Camptopoeum guichardi</i> Patiny 1999         | MU                         | 5-Oman            | <i>P. platymerus</i> Pérez 1895         | AG, TS                 | 2              |
| <i>C. handlirschi</i> Friese 1900                | AG, TS                     | 2-Chott El Djerid | <i>P. posticus</i> Warncke 1972         | IS, JO, SY             | 3              |
| <i>C. nadii</i> (Warncke 1972)                   | MO                         | 5-W. Morocco      | <i>P. pyropygus</i> Friese, 1901        | AG, IS, LY, MO, SA, TS | 1              |
| <i>C. negevensis</i> (Warncke 1972)              | IS                         | 5-S. Israel       | <i>P. runggii</i> Benoist 1937          | MO                     | 5-S. Morocco   |
| <i>C. pseudoruber</i> (Warncke 1987)             | MO                         | 5-S. Morocco      | <i>P. vachali</i> Pérez 1895            | AG, MO, TS, LY         | 2              |
| <i>C. simile</i> (Pérez 1895)                    | AG, IS, MO, TS             | 1                 | <i>Plestopanurgus zizus</i>             | MO                     | 5-S. Morocco   |
| <i>Clavipanurgus desertus</i> (Warncke 1987)     | MO                         | 5-S. Morocco      | (Warncke 1987)                          |                        |                |
| <i>C. gusenleitneri</i> Patiny 2004              | SY                         | 5-Syria           | <b>Rophitinae</b>                       |                        |                |
|  |                            |                   | <i>Rophites theryi</i> (Benoist 1930)   | MO                     | 5-W. Morocco   |
|  |                            |                   | <i>Systropha androsthenes</i>           | SA, TC                 | 3              |
|  |                            |                   | Baker 1996                              | MU                     | 5-Oman         |
|  |                            |                   | <i>S. diacantha</i> Baker 1996          | IS, TS                 | 1              |
|  |                            |                   | <i>S. hirsuta</i> Spinola 1839          | MO                     | 5-S. Morocco   |
|  |                            |                   | <i>S. maroccana</i> Warncke 1977        | AG, MO, TS             | 2              |
|  |                            |                   | <i>S. pici</i> Pérez 1895               |                        |                |

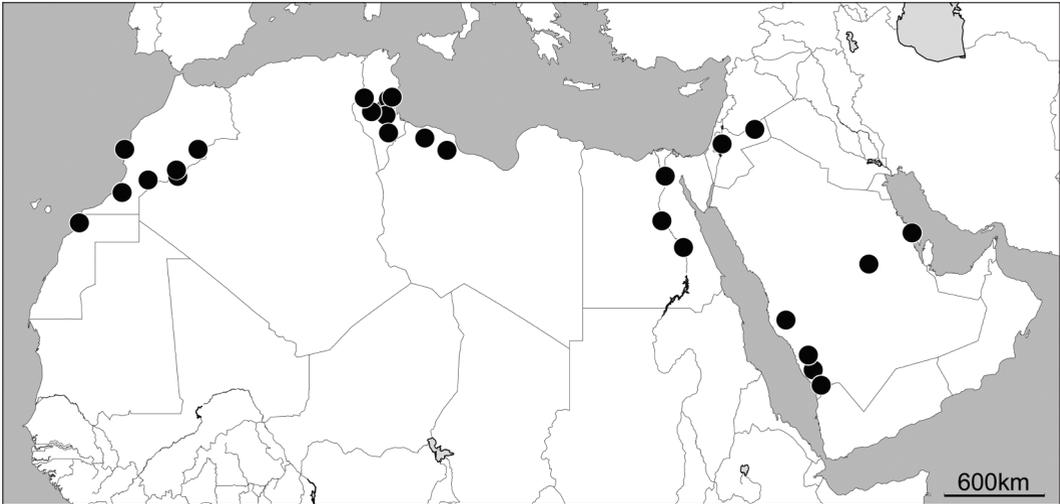


Fig. 6. Collecting localities of *Panurgus dentatus*.

*dentatus* is particularly illustrative of this kind of distribution (Fig. 6).

In the Arabian Peninsula, *P. dentatus* occurs along the Persian Gulf coast, in the Chotts (salt lakes) near Ad-Damman (26°25'N 50°5'E), and along the southwestern coast in Asir province. Inland, specimens were recorded in the Tuwayq Jebel (mountains) (near Riyadh, Saudi Arabia) and in northeastern Jordan (Al Mafraq area).

In north Africa the species was reported from

Egypt (Nile Valley), the mountains south of Tripoli (Tripolitania) and westwards into Tunisia (east of the Chott el Djerid). In Morocco, *P. dentatus* is found along the southern slopes of the Atlas Mountains, from Erfoud to Laayoune.

Several other species display a similar multilocal distributional pattern, but with asymmetries (slight topological divergences). For instance, *Dasygoda sinuata*, *Melitta aegyptiaca* and *Melitta schmiedeknechti* (Fig. 7) display a strong western

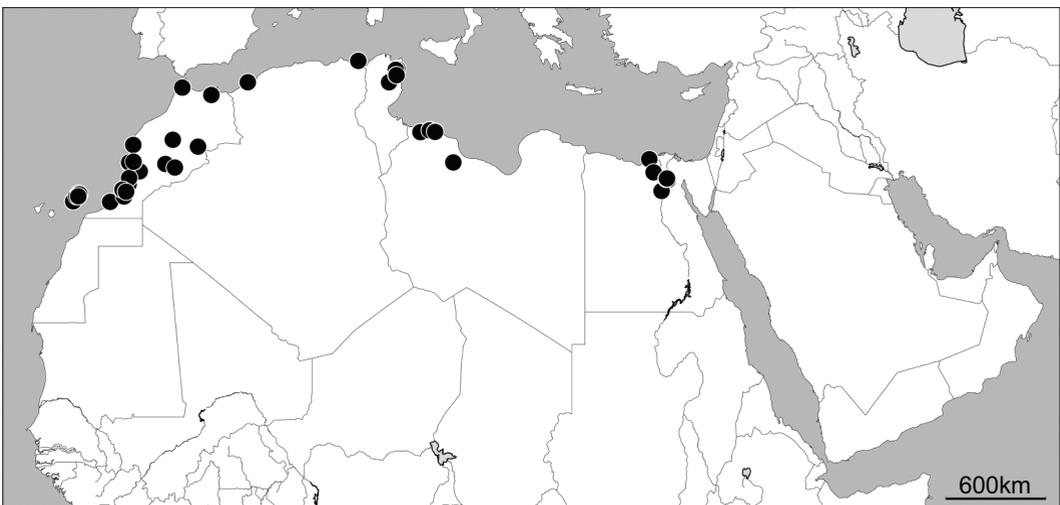


Fig. 7. Collecting localities of *Dasygoda sinuata*.

asymmetry due to their presence in the Canary Islands, from which all the other studied species are absent. *Melitturga oraniensis* and *Pararhophites quadratus* display also a multilocal distribution but are rare, restricted to a smaller number of localities than *P. dentatus* and absent from the Arabian Peninsula. The range of *Panurgus buteus* constitutes an interesting counter example. This species is unknown in western Morocco, but it is reported from the eastern High Atlas of Algeria and Tunisia. *P. buteus* is also frequent and abundant in the eastern part of the study area, notably in Jordan Valley. Likewise, *P. nirgriscopis* is known from Morocco (Riff Mountains and southwestern High Atlas), Egypt (Nile Valley), Jordan (Jordan Valley) and Oman.

*Mauritanian distributions.* – Another distributional pattern is displayed by 15 of the studied species, endemic to the Maghreb or part of this region (Table 2, Figs 8a,b). Unlike those species that are also present (but not endemic) in that part of SAD, the taxa with Mauritanian distributions are more frequent north of the Atlas than in the Pre-Saharan ecosystems. However, some show southward range extensions along the main river valleys and oases of the Drâa and Ziz (Fig. 1). These ecosystems define a fragmented area of overlapping distributions between the species extending south from primarily northern distributions, and those with stronger Saharan affinities. The distributions of *Panurgus calceatus* and *Panurgus farinosus* provide examples of this kind of distributional pattern (Fig. 8a).

In addition, several north African species are restricted to one part of the Maghreb or other.

*Dasygoda brevicornis* (Fig. 8b) and *Panurginus tunensis* are largely restricted to Tunisia and eastern Algeria (a few records from southern Morocco for *P. tunensis*). Conversely, *Dasygoda oraniensis* is restricted to Morocco and western Algeria and is seemingly absent from the eastern part of north Africa (Fig. 8b) and the distributions of these species follow topologically the Atlas Mountains (from Morocco to Tunisia). The disjunction between these two kinds of north African species is topologically centred on the Algerian depressions north of Biskra (34°54'N 5°43'E).

*Arabian distributions.* – This distributional pattern is the eastern equivalent of the previous one. Among the study species, *Dasygoda albipila* has the best-documented distribution and includes populations in Oman, Qatar, Saudi Arabia (near Riyadh) and southern Jordan Valley (Fig. 9). The distribution in the Arabian Peninsula displayed by *D. albipila* is very close to that of other species ranging into that part of SAD (e.g. *Panurgus dentatus*).

Many of the apparent limited distributions in the Arabian Peninsula are probable artefacts resulting from a lack of data. However, some good examples of typical Arabian patterns can be observed. For instance, *Panurgus posticus* has been recorded in Israel and Western Jordan, where it is sympatric with *Dasygoda albipila*, *Panurgus dentatus*, *Panurgus nirgriscopis*, *Camptopoeum sacrum* Alfken, *Clavipanurgus orientalicus* Warncke. The range of these species also includes several isolated populations in northeastern Jordan and in the Tigris Valley, but are not reaching the eastern part of the

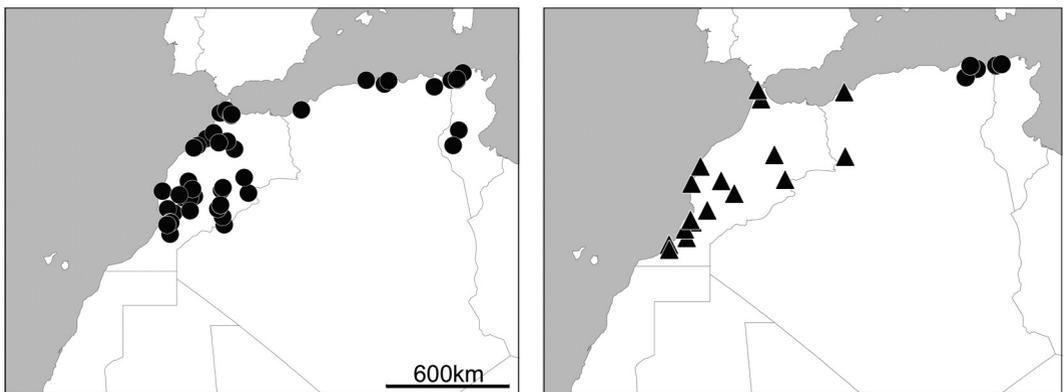


Fig. 8. a. Collecting localities of *Panurgus calceatus*; b. Collecting localities of *Dasygoda brevicornis* (circles) and *Dasygoda oraniensis* (triangles).

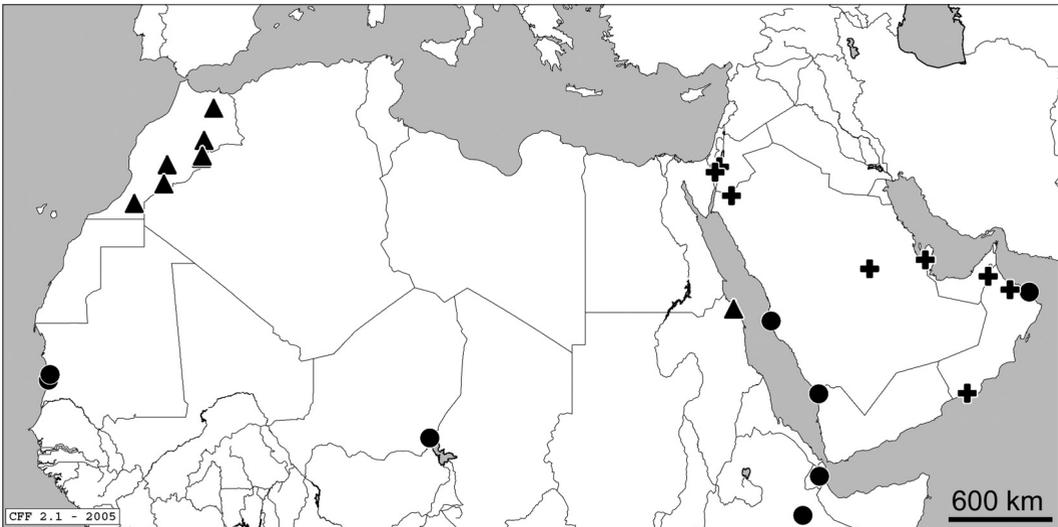


Fig. 9. Distribution of *Borgatomelissa brevipennis* (circles), *Dasypoda albipila* (crosses) and *Promelitta alboclypeata* (triangles).

Arabian Peninsula. On the contrary, the Oman endemic *Systropha diacantha* could serve to define an Eastern Arabian pattern.

**Sahelian distribution.** – The distributions of *Promelitta alboclypeata* and *Borgatomelissa brevipennis* (Fig. 9) include populations in Djibouti (*B. brevipennis*), Egypt (*P. alboclypeata*), Ethiopia (*B. brevipennis*), Saudi Arabia (*B. brevipennis*), Morocco (*P. alboclypeata*) and Mauritania (*B. brevipennis*). Recently, *B. brevipennis* has been recorded from the northwest shores of Lake Chad (Niger). These data suggest that both species may have dispersed across the southern Sahara along the Sahelo-Sudanian plant region. This distributional pattern is anecdotal among the studied species but similar distributional patterns have been documented for various other species among the Nomiinae and Nomioidinae (Pauly 1990; Pesenko & Pauly 2005).

**Local distributions.** – 27 of the species studied (Table 2) are local endemics in SAD (restricted to one or a few close localities). The available information shows that the distribution of these taxa cannot be attributed to the same causes. The knowledge of the distributions of such species as *Clavipanurgus gusenleitneri*, *Dasypoda syriensis* *Meliturgula senegaliae*, *Meliturgula denesia* is too sketchy (in some cases limited to the type locality) to be discussed further.

On the contrary, the distributions of several other endemic species are particularly informative. *Fidelia ulrikei* and *Plesiopanurgus zizus* display a strong concentration of their populations in the oueds (non-permanent rivers) Drâa and Ziz Valleys (Morocco) respectively (Fig. 10). Likewise, in the western part of the Arabian Peninsula, species like *Camptopoeum negevense*, *Clavipanurgus gusenleitneri* and *Melitturga krausi* are endemic to the Jordan Valley. It is noteworthy that the widely distributed taxa present in the Arabian Peninsula also occur in these areas of endemism.

Numerous other endemic patterns are observed in SAD. In Morocco, species like *Camptopoeum nadigi*, and *Rophites theryi* range chiefly in the Atlantic area. To the south, *Panurgus acutus* and *Panurgus minor* (subgenus *Micropanurgus* Patiny 2002) are restricted to the Acacia-Argania woodland area of the Souss Valley in south Morocco. Finally, others like *Lithurgus cephalotes* are seemingly restricted to more elevated parts of the Atlas range.

In Algeria, *Avpanurgus flavofasciatus* has only been recorded in the Chotts area near Taguine (Fig. 10). The distribution of this species (cf. *Camptopoeum handlirschi*) can be topologically related to the Pre-Saharan depressions, which seems to separate the distributions of several west and east North African species.

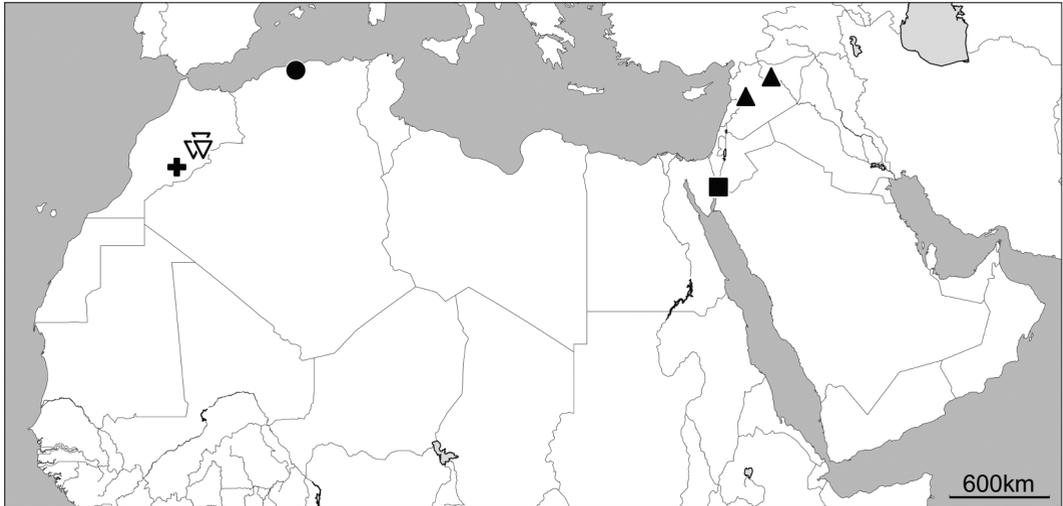


Fig. 10. Collecting localities of *Avpanurgus flavofasciatus* (circle), *Dasypoda gusenletieni* (square), *Dasypoda syriensis* (dark triangles pointed up), *Fidelia ulrikei* (cross) and *Plesiopanurgus zizus* (white triangles pointed down).

Likewise, in Oman, Djebel Akdhar (in the north) and the Dhofar area (in the south-east) constitute similar areas of endemism notably characterised by the presence of *Camptopoeum guichardi* and *Systropha diacantha*.

## Discussion

### 1. Diversity and endemism rate

The high levels of generic diversity, species endemism (O, R) and species diversity (D) (Table 1) suggest that the overall diversity of bees in SAD would be close to those of other subregions with remarkably diversified bees faunas, like California, northern Mediterranean Basin and Central Asia (Table 1).

In addition, the inverse relationships observed between indices calculated in the generic and specific levels, provide insights on the biogeographical history of SAD. If we hypothesise that divergence at the generic level constitutes evidence for an older isolation than species divergence, the low level of generic endemism is suggestive of an ancient isolation followed by a period of relaxed migration. On the contrary, the high level of specific endemism suggests recent and strong isolations, having been punctually relaxed as indicated by the width and fragmentation of the distribution

of some taxa (e.g., *P. nigroscepus*). Consequently, the previous observations (and the results in Patiny et al. (in preparation) and Pesenko & Pauly (2005)) support the hypothesis of successive periods of faunal exchange and segregation between SAD and neighbouring areas. These cycles of isolation and relaxed exchanges can be related to the cycles of climate changes undergone by SAD (see above: bioclimatological sketch).

### 2. Biogeographical relationships

Previous results, allied with the current knowledge of the phylogeny of the studied groups, give a strong insight into the biogeographical links between SAD and the adjacent areas (northwestern Palearctic, subsaharan Africa, and Central Asia).

Connections between SAD and southwestern Europe, have been discussed in numerous previous papers (De Lattin 1967; Hewitt 1999; Patiny & Gaspar 2000a,b; Patiny et al. 2005). Among the studied species, the distributions of groups like *Pachycephalopanurgus* exemplify the ways in which NNE can have worked between SAD and the adjacent areas. The NNE must be considered as a mechanism able to act quickly during short contact periods between closely adjacent areas.

According to the usual (even if highly discussed) hypothesis of a geographical coincidence

between the taxa's highest diversity and its evolutionary origin (Sagarin & Gaines 2002), the example of *P. (Pachycephalopanurgus)* suggests also that the SAD (at least the western part) is the source of a significant number of western Palaearctic taxa. The NNE provides thus an explanatory mechanism for the movements of the species both in and out of the study area. Other examples are documented in *Dasypoda*, *Melitta*, *Melitturga* and *Rophites* (Michez et al. 2004b; Patiny & Gaspar 2000a).

Conversely, the distribution of several species demonstrates the existence of long distance (trans-Saharan) isolations of populations either before or after speciation. Examples are found in subsaharan taxa: *Lithurgus pullatus*, *Melitturga albescens* (e.g.) and Central Asian species: *Clavipanurgus desertus*, *Plesiopanurgus zizus*. The formation of such disjunct patterns between widely separated populations probably resulted from repeated expansion and contraction of distribution ranges under cyclical climatic changes (contrary to NNE). Such changes were punctually undergone by SAD during the whole Tertiary-Quaternary period (Marchant & Hooghiemstra 2004; see above: bioclimatological sketch) and it is probable that they impacted directly on the ranges of the studied taxa.

### 3. Distributional patterns

The ecological link between the bees and the xeric ecosystems reported by most previous authors (Michener 1979, 2000; Radchenko & Pesenko 1994; Roubik 1989), is also reflected in our results. The collecting localities of the studied species are mostly located within the range of the Mediterranean- and Pre-Saharan-like ecosystems (Adams & Faure 1997; NGS 2001; Olago 2001; White 1986) (Fig. 1). The ranges of *Borgatomeissa brevipennis* and *Promelitta alboclypeata*, follow exactly the Sahelo-Sudanian ecosystems. None of the studied species occur preferably in harsh desert environments and Fig. 5 shows that the highest diversities are encountered in Mediterranean and Pre-Saharan areas. This figure suggests an unusual south-north latitudinal gradient in the studied species.

Our results allow a more accurate definition of the distributional patterns of the studied species within their favoured ecosystems. The xerophilous preference of bees is one general trait of these insects, but, within the temperate warm xeric eco-

systems, populations are typically concentrated in some kinds of favoured areas:

1. The mountains extending within SAD (Figs 6, 7): the Atlas Mountains, the northwestern Libyan plateau and the western chains in Saudi Arabia and Yemen (most species);
2. The mountains dotting the central desert part of SAD: Hoggar, Tibesti (Sahara), Tuwayq (Nedjd) (*Melitturga albescens*, *Panurgus dentatus*);
3. The streams and river valleys (Figs 4a, 6, 10): the Nile (Egypt), the Jordan and several other oueds and rivers (*Fidelia ulrikei*, *Lithurgus pullatus*, *Panurgus calceatus*, *Plesiopanurgus zizus*, *Uromonia stagei*);
4. The coasts (*Dasypoda albipila*, *Dasypoda brevicornis*) (Figs 6, 10).

The causes of these biogeographical hotspots are probably numerous and, at least partly, linked to various components in the ecology of each species (Tews et al. 2004). They could consequently not be comprehensively listed on the sole basis of the previous results. However, some of them can be examined in a Grinnellian way, testing the correspondence between some limiting factors and the taxon ranges (Grinnell 1917; Parmesan et al. 2005).

Studies on many taxonomic groups proved that the climatic and bioclimatic factors, such as temperature, moisture or evapotranspiration can be correlated to species richness because they not only limit the species distribution, but also the resource availability (Andrews & O'Brien, 2000; Ceballos & Brown 1995; Gorodkov 1986a,b, 1990, 1992). In the general xeric context of the studied distributions, the water availability, depending on climate and microclimates and conditioning plants distributions, is one potentially powerful limiting factor for bee distribution (Gess 1992; Mayer & Kuhlmann 2004; Sole et al. 2005). We cannot show that the studied species are directly influenced by the water availability. However, we can reasonably hypothesise that they indirectly depend on water through their food resources (flowering plants).

The study of the ecological characteristics of the precise sites from which the individual species are found suggests a relation between the water (and floral resources) availability and species richness.

## Conclusions

The study area is characterised by high species diversity and endemism rates. The indices used show that the SAD is a core area for bee diversity. On the other hand, when we consider the biogeographical affinities of the studied faunas with the other areas in the Eastern Hemisphere, the main part of the study territory fauna seems resulting from a NNE, involving the other parts of the Western Palaearctic as classically observed in many other living groups (Cox & Moore 2005). However, influences of more distant areas, like Central Asia and the sub-Saharan region, are also significant, notably in the contribution to the SAD's endemism.

The disjunctions observed in the distributions of these taxa with more distant origins leads us to search for explanatory hypotheses regarding the dispersal mechanisms within the study area. These distribution patterns are best explained by cycles of repeated expansions and fragmentations of species ranges, in some cases perhaps followed by extirpation or speciation. The historical changes in the climate of the SAD are probably the best arguments to explain these distribution patterns. The differentiation of eastern and western faunas (Mauritanian and Arabian patterns) can be explained in the same way.

Another conclusion is the existence of a limited number of distributional patterns displayed by the species ranges in SAD. Interestingly, these patterns fit not only to the distributions of the studied species, but also more generally to these of numerous taxa like *Epeolus* (Eardley 1991a), *Nomada* (Eardley & Schwarz 1991), *Nomiinae* (Pauly 1990) or *Nomioidinae* (Pesenko & Pauly 2005). Within these patterns, species are distributed in spots characterised by some shared ecological traits, notably higher moisture/precipitation rates than in the surrounding areas. These conclusions lead us to define bees as typical xeric taxa with seemingly moisture-conditioned distributions. Moreover, at a finer geographical scale, SAD can be described as a web of biogeographically interconnected high diversity hotspots (Fig. 5), resembling "terrestrial islands" and behaving biogeographically like true islands.

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