Contemporary distributions of *Panurginus* species and subspecies in Europe (Apoidea: Andrenidae: Panurginae)

Sébastien Patiny

Abstract

The largest number of Old World *Panurginus* Nylander, 1848 species is distributed in the West-Palaearctic. The genus is absent in Africa and rather rare in the East-Palaearctic. Warncke (1972, 1987), who is the main author treating Palaearctic Panurginae in the last decades, subdivided *Panurginus* into a small number of species, including two principal taxa admitting for each a very large number of subspecies: *Panurginus brullei* (Lepeletier, 1841) and *Panurginus montanus* Giraud, 1861. Following recent works, the two latter are in fact complexes of closely related species. In the West-Palaearctic context, distributions of certain species implied in these complexes appear as very singular, distinct of mostly all other Panurginae ranges and highly interesting from a fundamental point of view. Based on a cartographic approach, the causes which influence (or have conditioned, in the past) the observed ranges of these species are discussed.

Key words: Panurginae, biogeography, West-Palaearctic, speciation, glaciation.

Introduction

In the Old World Panurginae fauna, *Panurginus* Nylander, 1848 is one of the only two genera (with *Melitturga* Latreille, 1809) which are distributed in the entire Palaearctic region. The genera *Camptopoeum* Spinola, 1843 and *Panurgus* Panzer, 1806 are also represented in the East-Palaearctic (in northern Thailand), but too few data are available for these genera to make them the subject of particular considerations.

From the biogeographical point of view, *Panurginus* is even more singular in being the only Holarctic Panurginae genus. In spite of this particularly wide range, most of the known Old World *Panurginus* species are concentrated in the West-Palaearctic region.

As the largest part of the West-Palaearctic Panurginae systematics, the knowledge of *Panurginus* is mainly reported in Warncke's works (1972, 1987) and reviewed by some authors (Patiny 1999, 2001, Rasmont et al. 1995, Schwarz et al. 1996). According to all authors, two major species groups exist (and some other independant species), which were considered by Warncke as species including a large number of subspecies.

The taxa *Panurginus montanus* Giraud, 1861 sensu lato and *Panurginus brullei* (Lepeletier, 1841) sensu lato are studied in the present paper. The numerous particularities of their distributions are characterized and discussed here. The limits of these distributions were proposed and related to the contemporary and past developments which could have caused these ranges.

Catalogue of the old world species of *Panurginus*

Panurginus Nylander, 1848
- Type species: *Panurginus niger* Nylander, 1848
- = *Panurginus* Nylander, 1848
- = *Scrapteroides* Gribodo, 1894
- = *Panurgus* (*Panurginus*) (Nylander, 1848) in Warncke (1972).
- = *Panurginus* (*Panurginus*) Nylander, 1848 in Ruz (1986)

Panurginus albopilosus Lucas, 1849
- = *P. annulipes* Lucas, 1849
- = *P. politus* Benoist, 1937
- = *Panurgus* (*Panurginus*) *albopilosus* Lucas, 1849 in Warncke (1972)

Panurginus alpinus Warncke, 1972
- = *Panurgus* (*Panurginus*) *montanus alpinus* Warncke, 1972

Panurginus alticolus Morawitz, 1876

= *Panurgus* (*Panurginus*) *montanus alticolus* Morawitz, 1876 in Warncke, 1972

Panurginus annulatus (Sichel, 1859)
= *P. difformis* Gribodo, 1894
= *P. halictoides* Gribodo, 1861
= *Panurgus* (*Panurginus*) *brullei annulatus* (Sichel, 1859) in Warncke, 1972

Panurginus brullei (Lepeletier, 1841)

Panurginus clarus Warncke, 1987
= *Panurgus* (*Panurginus*) *brullei clarus* Warncke, 1987

Panurginus corpanus Warncke, 1972

Panurginus herzi Morawitz, 1892
= *Panurgus* (*Panurginus*) *montanus herzi* Morawitz, 1892 in Warncke, 1972

Panurginus labiatus (Eversmann, 1852)
= *Panurgus labiatus* Eversmann, 1852
= *Panurgus clypeatus* Eversmann, 1852
= *P. arenarius* Schenck, 1861.

Panurginus lactipennis Friese, 1897

Panurginus minutulus Warncke, 1987

Panurginus montanus Giraud, 1861

Panurginus ponticus Warncke, 1972
= *Panurgus* (*Panurginus*) *montanus ponticus* Warncke, 1972

Panurginus picipes Morawitz, 1890

Panurginus romani Aurivillius, 1914

Panurginus schwarzi Warncke, 1972
= *Panurgus* (*Panurginus*) *brullei schwarzi* Warncke, 1972

Panurginus sericatus Warncke, 1972
= *Panurgus* (*Panurginus*) *montanus sericatus* Warncke, 1972

Panurginus tunensis Warncke, 1972
= *Panurgus* (*Panurginus*) *brullei tunensis* Warncke, 1972

Panurginus turcomanicus Popov, 1936
= *Panurgus* (*Panurginus*) *brullei bytinski* Warncke, 1972

Panurginus tyrolensis (Richards, 1932)
= *Panurgus* (*Panurginus*) *montanus tyrolensis* (Richards, 1932) in Warncke, 1972

The distribution of *Panurginus* around the Mediterranean basin

The distribution of the genus *Panurginus* around the Mediterranean basin is shown in fig. 1.

Fig. 2 shows the distribution of three species associated by Warncke in the *Panurginus brullei* complex: *Panurginus albopilosus*, *P. annulatus* and *P. tunensis*. These ranges characterize the three kinds of *Panurginus* distribution in the western part of the Mediterranean basin. *Panurginus albopilosus* is typically Ibero-Maghrebian, *P. annulatus* is strictly Spanish and *P. tunensis* is only Maghrebian.

Fig. 3 shows the distribution of *P. labiatus* and *P. lactipennis* in the Balkan and Turkey.

Fig. 4 shows the distribution of four species pooled by Warncke in the *Panurginus montanus* complex: *P. alpinus*, *P. montanus*, *P. sericatus* and *P. tyrolensis*. These species exhibit a strong typicity of their distributions in the different Alpine and Balkanic mountain chains. *Panurginus alpinus* is a French species, the most occidental of the complex. *Panurginus montanus* and *P. sericatus* have a wider and more eastern distribution in the Alpine chain. *Panurginus tyrolensis* is a Balkanic taxon.

Discussion

Panurginus species are not uniformly distributed in the West-Palearctic and around the Mediteranean basin. The generic distribution presents three large disjunctions (fig. 1): a first one between the Alps and Spain (including the Pyrenees), an other at the Transdanubian plain between the Alpine and Balkanic populations and the third between western Lybia and southern Israel. All these disjunctions must not be considered *a priori* as homologous and have to be explained by clear argumentations.

The absence of *Panurginus* between Spain and the Alps (fig. 1) is easily understandable and may be described as the consequence of the characteristics of the different taxa. Firstly, the Iberian species (fig. 2) generally are strongly xerophylous and thermophylous (Patiny 2001, Patiny & Gaspar 2000). In France the climatic conditions rarely are favourable for these species, even in the Mediterranean area. Secondly, their distribution is restricted by the Pyrenean obstacle which only allows the migration of such species from time to time, for example in particular climatic configurations. In the east, the French *Panurginus* species (fig. 4) is strictly a mountain taxon which is unknown below 1500m altitude and apparently missing in the Pyrenees. These observations suggest that the central part of France is quite unfavourable to *Panurginus* expansion.

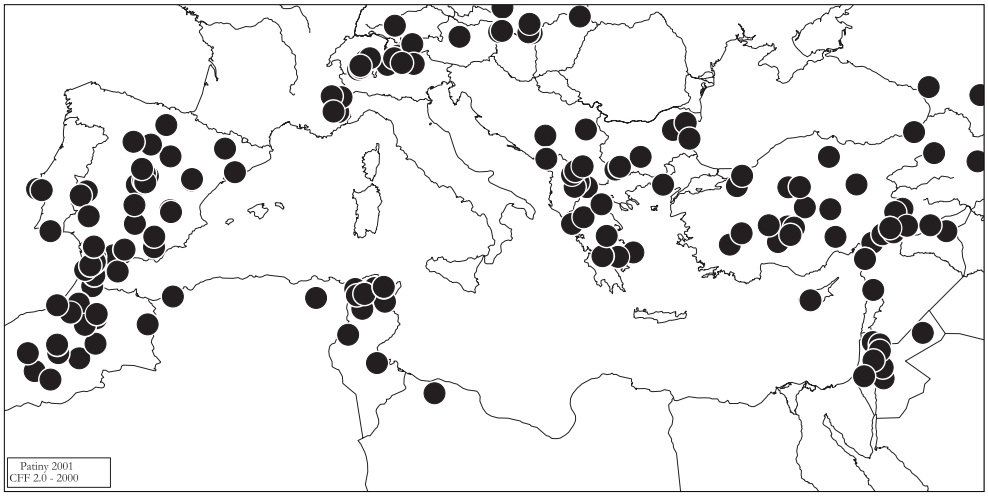

Figure 1
Distribution of the genus *Panurginus* around the Mediterranean basin.

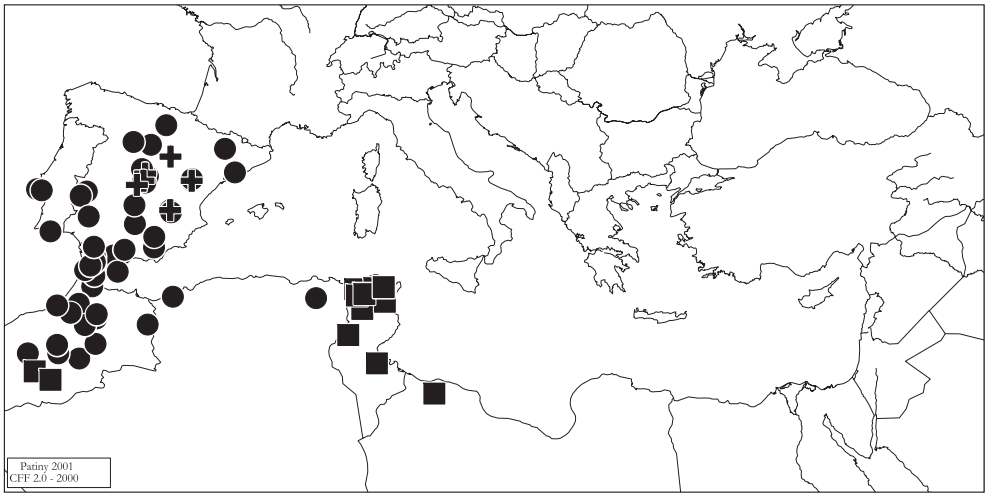

Figure 2
Distribution of three species of the *Panurginus brullei* complex: *Panurginus albopilosus*, *P. annulatus* and *P. tunensis*.

The second disjunction in the generic distribution is centered at the level of the Transdanubian plain (fig. 1, 3, 4). Once again, the mountain character of the *P. montanus* species group (fig. 4) may reliably explain the absence of these species in the plain. Endemic species related to *P. montanus* occur in the entire area surrounding this plain but none of those is found in the plain itself. The altitude can be considered to be the limiting factor of the concerned distributions. In cases of other species, we could also consider that the observed interruption can be the consequence of a lack of data. For example, *Panurginus labiatus* (fig. 3) is not a typical mountain species but it is also distributed on each side of the disjunction. It seems likely that this disjunction can at least for

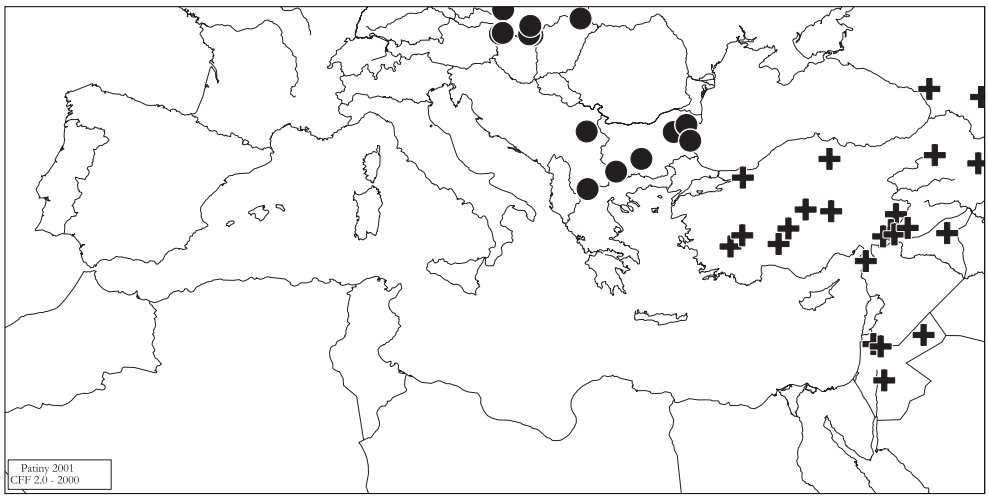

Figure 3
Distribution of *Panurginus labiatus* and *Panurginus lactipennis* in the Balkan and Turkey.

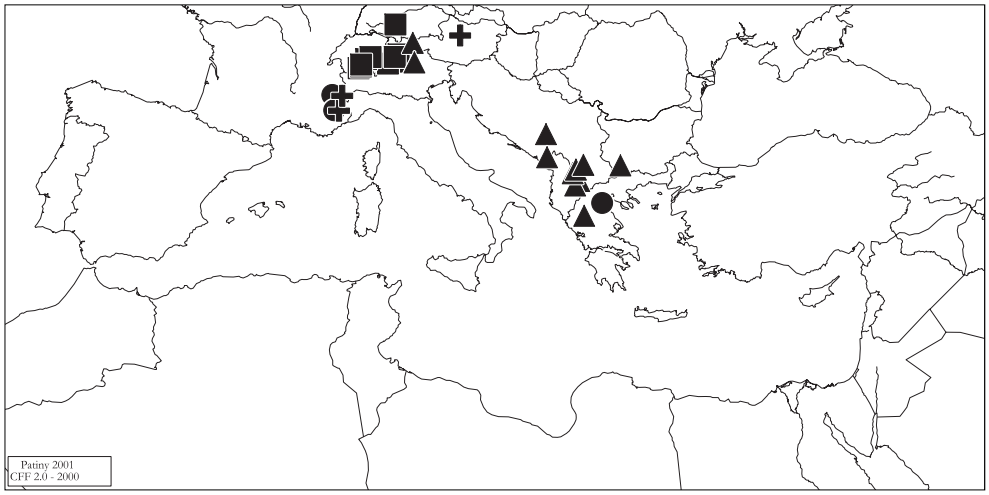

Figure 4
Distribution of four species of the *Panurginus montanus* complex: *Panurginus alpinus*, *P. montanus*, *P. sericatus* and *P. tyrolensis*.

some taxa be explained by a lack of data.
Panurginus species are not known between western Lybia and southern Israel (fig. 1, 2). Disjunctions of ranges in this part of North-Africa have been observed in numerous other groups. The relatively greater extension of the Sahara (and more generally this of desert ecosystems) can be considered to act against a larger distribution of the species in this part of North-Africa. In some other groups (for example in *Panurgus* Panzer, 1806) some intermediar isolated areas (this area is characterized by a high level of endemism, notably in Cyrenaika) and a wider distribution in eastern Egypt are observed. Perhaps

this could also be revealed for *Panurginus* by an improvement of knowledge, keeping in mind that the main part of the disjunction would probably remain empty of any data.

Beside these major disjunctions, *Panurginus* species show several local concentrations acting in the West-Palaearctic frame as diversity pockets. *Panurginus albopilosus*, *P. annulatus* and *P. tunensis* (fig. 2) characterize one of the most important of these centers, the Ibero-Maghrebian. A more detailed study of the *Panurginus* ranges in the Ibero-Maghrebian area allows to distinguish different obvious origins and distribution patterns of the taxa. *Panurginus albopilosus* is almost equally distributed in southern Spain and northern (Atlantic) Morocco. *Panurginus annulatus* is restricted to Central Spain, while *P. tunensis* is typically Maghrebian, distributed along the southern slopes of the Atlas in Tunisia and Morocco (the rarity in Algeria should be considered as the direct consequence of a lack of data). The Ibero-Maghrebian frame which appears, by means of more general approaches (Patiny 2001, Patiny & Gaspar 2000), as a major dispersion and diversification centre for many Panurginae, is in fact composed by several small entities, partly characterized here based on *Panurginus* distributions. These areas are localised in Spain, northern Maghreb or the southern Atlas. It has to be mentioned that, closely related to the continental area by their fauna, the Canary islands can be described as a fourth area of isolation for Ibero-Maghrebian Panurginae. A reliable illustration is the range of *Panurginus brullei*.

Turkish species were deliberately chosen not to be entirely studied here. Previous studies (Oosterbroek & Arntzen 1992, Patiny 2001, Patiny & Gaspar 2000, Varga 1996) clearly show the high interest of Turkey and neighbouring areas for West-Palaearctic biodiversity problematics. This area obviously needs specific studies, because of its high biodiversity. Nevertheless, the Turkish species *P. lactipennis* is studied here in association with *P. labiatus*. These taxa ranges illustrate a particular aspect of the role of Turkey in the diversification of Panurginae. From the morphological point of view, *P. labiatus* was clearly observed to be the probable sister-group of *P. lactipennis* joined to its related species. Meanwhile, *P. lactipennis* is strictly distributed in Turkey and the oriental neighbouring area, while *P. labiatus* is strictly Balkanic. This importance of the Balkanic area in the diversity and diversification of *Panurginus* is quite exceptional, most other Panurginae being rather poorly diversified in this region. It is also well underlined by the case of *Panurginus montanus* and related species. Studying these taxa, specific divergences were observed all around the transdanubian plain in the different mountain chains. *Panurginus alpinus* has a western distribution, restricted to the western part of the Alpine chain. *Panurginus montanus* and *P. sericatus* are more Central-European but also strictly restricted to the Alps. In the southern Balkan, *Panurginus tyrolensis* is mainly distributed in the Pindos chain. All distributions seem to indicate that the *Panurginus montanus* group has diversified around the transdanubian plain. The Balkan can thus be designated for some Panurginae, *Panurginus* for example, as a centre of diversification and dispersion, as it is for numerous other groups (Fritz 1996, Hewitt 1999, De Lattin 1967, Reinig 1937, 1969).

The research on the causes of the contemporary biogeographic configurations generally – and in Apoidea in particular - lead to the Quaternary glaciations and their faunal implications. These phenomena constitute a particularly interesting explanation of the diversification of Apoidea. The two processes have indeed been fully contemporary. The Apoidea s.str. diverged from the Sphecoidea s.str. in late Secondary and their diversification took place during Tertiary and Quaternary (Engel 2001, Michener 2000, Radchencko & Pesenko 1994). The contemporary species can generally be considered as the result of a late Quaternary specification process (consequence of the Würm glaciation).

During glaciations following a now relatively well known process, a large ice sheet covered the southern Palaearctic. This northern ice sheet was followed by a large zone of tundra-like ecosystems which is totally unsuitable for survival of numerous species, in particular for the Apoidea. The two main consequences of these eco-climatic transformations are the extinction of most stenotypic taxa and the restriction of the more eurytopic species to small disconnected refugia distributed in meridional parts of conti-

nents (around the Mediterranean basin in case of the West-Palaearctic area). Other consequences of glaciations are notably the possibility of slight southward expansion due to the reduction of the sea level. The transformation of the distributions under the pressure of glaciations appears to be clearly favourable to diversification.

The observed restriction of the species related to *Panurginus albopilosus* to the Ibero-Maghrebian area is also particularly well explained and illustrated by this climatic transformation scheme. All available representations of ranges of ecosystems during the last glacial optimum show that the large general Ibero-Maghrebian refugium is in fact fragmented into several small entities (Hewitt 1999, Varga 1996). Distinct areas were distributed from Central Spain to the southern coast. Morocco was at least subdivided into two parts: a North-West Atlantic plain and the southern slopes of the Atlas, limited by desert in the south. A third entity seems to have been constituted by the Oued Souss plain (Southern Agadir). In the same complex of refugia the particular place occupied by the Canary Islands characterized by several endemic species and subspecies had to be observed. The Spanish endemism of *P. annulatus* can then be explained as the consequence of isolation in one of the Spanish refugia. The case of *P. albopilosus* case is more difficult to explain. This species is distributed in the whole Ibero-Maghrebian area and does not show any notable polarity. Meanwhile, this species was observed to be nearly exclusively distributed in the northern Atlas and particularly abundant in northern Morocco. This species could be considered as truely Moroccan, so it could only be an Atlantic taxon. Opposite to *Panurginus albopilosus*, *P. tunensis* is only present in Tunisia and southern parts of the Moroccan High Atlas, following a long peri-Saharian and trans-Maghrebian diagonal. A probable origin of this species is situated in the southern Atlas. *Panurginus brullei* is an endemic Canarian species, very probably the consequence of a population isolation in these islands.

Likewise, the segregation between *P. labiatus* and *lactipennis* can be easily explained in the same way. During glaciations the Balkan Peninsula constituted a refugium area separated from Turkey. This could have lead to the differentiation of *P. labiatus* while the relative homogeneity of the Balkanic refugium was not favourable to further speciation. Contrary to the Balkanic area, southern and eastern parts of Asia Minor are crumbled into numerous small refugia. This could be used to explain the diversification within the *Panurginus lactipennis* group.

West-Palaearctic species related to *Panurginus montanus* are mainly Balkanic and Central-European and distributed in the main mountain chains. In regard of this typical distribution, implying colder habitats than usual for Panurginae, it is plausible to presume that the origins of this species are probably different of the usual mediterranean refugia. During glaciation, between the periglacial tundra and the mediterranean relict habitats, there were intermediar ecosystems. The *pseudoperiglacial cold steppe* and *forest-steppe belts* as mentioned by Varga (1996) could have provided refugia for species featuring the ecological preferences of *Panurginus*. This hypothesis gains strength if the observed disjunction (fig. 4) between *P. tyrolensis* and the other species would correspond with the existence of a *pseudoperiglacial cold steppe* and *forest-steppe* isola in the Balkanic area.

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S. Patiny
Faculté universitaire des Sciences agronomiques de Gembloux
Service de Zoologie générale et appliquée
Passage des Déportés 2
B-5030 Gembloux
Belgium
patiny.s@fsagx.ac.be