Biogeographia – The Journal of Integrative Biogeography

Title

The Mediterranean-southern African disjunct distribution pattern in the scarab beetles: a review (Coleoptera Scarabaeoidea)

Permalink

https://escholarship.org/uc/item/6d6769d6

Journal

Biogeographia – The Journal of Integrative Biogeography, 29(1)

ISSN

1594-7629

Author

Carpaneto, Giuseppe M.

Publication Date

2008

DOI

10.21426/B6110110

Biogeographia vol. XXIX - 2008
(Pubblicato il 30 dicembre 2008)
The Mediterranean-southern african disjunct distribution pattern

The Mediterranean-southern African disjunct distribution pattern in the scarab beetles: a review (Coleoptera Scarabaeoidea)

GIUSEPPE MARIA CARPANETO
Dipartimento di Biologia Ambientale, Università degli Studi Roma Tre,
viale G. Marconi 446, 00146 Roma, Italy;
e-mail: carpanet@uniroma3.it

Key words: Biogeography, Afrotropical Region, Mediterranean Subregion, distribution range

SUMMARY

A survey of the distribution ranges currently shown by the scarab beetles was conducted by a review of literature data, in order to find clues or evidence of a Mediterranean-southern African distribution pattern, through a phylogeographic discussion. The results of the survey showed that the questioned distribution pattern in the scarab beetles was mainly referred to incorrect hypothesis of relationships due to convergence in morphological characters.

INTRODUCTION

A taxon with a disjunct distribution includes two or more groups that are phylogenetically related but widely separated from each other geographically. Such a model can be applied to isolated populations of a single species or to allopatric species of a single genus and so on, according to the rank of the taxon considered.

Disjunct distributions among taxa have intrigued biologists for decades. Most authors have invoked both dispersal and vicariance models to explain disjunct distribution. However, a disjunct distribution can be erroneously suggested by either an incorrect hypothesis of relationship due to convergence in morphological characters or a gap of knowledge in the geographical distribution of the taxa. An appropriate approach to test the model is to use molecular phylogenetic methods with an appropriate taxon sampling. Many molecular phylogenetic studies on several taxonomic groups of animals with disjunct distribution suggested that morphological convergence may be quite common. Therefore, the rational way in studying disjunct distributions is to determine if the observed pattern is real (true disjunction), nor due to convergence i.e., an artefact of incorrect taxonomy (false disjunction).

In many taxonomic groups of plants and animals, there are cases of disjunct distribution which show a clear discontinuity in the geographic range of apparently closely related taxa occurring in Europeo-Mediterranean countries and in tropical Africa respectively, with a wide gap throughout the Saharo-Sahelo-Arabic arid zone. This pattern is easily explainable by desertification which brought to extinction population and/or species of these taxa. On the other hand, some taxonomic groups show an extremely reduced version of this common distribution pattern because their occurrence is limited to the Mediterranean belt of Africa and to the southern end of the continent (de Winter, 1971). Such a polarized north-south distribution has been recorded in several groups of Coleoptera belong to different families (cf. Balthasar, 1963; Endrody-Younga, 1978; Holm, 1978, 1979).

The aim of this paper is to make a survey of the distribution ranges currently shown by the scarab beetles, in order to find clues or evidence of a Mediterranean-southern African distribution pattern, through a phylogeographic discussion.

The model

A comparison between the geographic range of many animals and plants, allowed to recognize four major distribution patterns of the Mediterranean-south African distribution pattern:

species with a disjunct Mediterranean-south African distribution pattern;
genera or supraspecific taxa with a disjunct Mediterranean-south African distribution pattern;
genera or supraspecific taxa with most species occurring in Mediterranean and south African areas, but also few (usually rare of localized) representatives in Eastern Africa;
genera or supraspecific taxa with species occurring from the Mediterranean areas to the Middle East of Asia (sometimes up to Central Asia), and in the arid corridor of eastern and southern Africa, from Somalia to Namibia.

The first pattern includes species which show a very clear disjunct pattern, with populations spread around the Mediterranean basin, sometimes extended to the Near and Middle East Asia. This pattern is very rare and may be explained by a recent event of dispersal from southern Africa to the Mediterranean basin (or vice versa), followed by the entire or partial extinction of populations in the intermediate areas, i.e. the East African provinces. A false disjunct pattern may be also suggested for species liable to be introduced by man.

The second pattern is a replicate of the first one at a higher taxonomic rank. It may be explained by vicariance followed by speciation events and then extinction of taxa from the intermediate areas of the generic range, i.e. from the East African provinces.

The third pattern is a particular case of the second one: a rational explanation of this model assumes the extinction from Eastern Africa of most the species assigned to the group. The few, often rare, survived species bear witness to the biogeographic history of the genus and represent a track of its past distribution.

The fourth pattern differs from the third one for the enlargement of the involved area to the Palearctic Region and the possibility of either an African or Asiatic origin, followed by dispersion from each continent to the other one. This pattern fits well to species adapted to a wide range of arid environments, from dry savannas to steppic highlands, that used the Arabic peninsula as a bridge.

The scarab beetles

The scarab beetles (Coleoptera Scarabaeoidea) are one of the most successful groups of beetles and includes approximately 27,800 species described throughout the world (Ratcliffe & Jameson, 2004), most of them living in subtropical and tropical areas. They are a conspicuous component of the biological communities and play different roles in the dynamics and structure of terrestrial ecosystems of all the continents, feeding on plants, organic decaying matter (rotten wood, humus, dung, carrion), mushrooms, and other invertebrates.

In this paper we attempted to trace the Mediterranean-south African model in the scarab beetles through the examination of their current distribution patterns, and to relate these with the climatic changes which affected the African environments and the dispersion routes for the animals during the Cenozoic Era (last 65 My). The main scope of the present paper is to screen all the scarab genera or species groups that show this distribution pattern and to gather the information available on their taxonomy and phylogeny with the aim to review all information on this subject in order to assess the contribution of this group to the model testing and to work out focuses for future research. A special attention was given to the groups which underwent a reliable systematic revision by cladistic or molecular approaches, in order to avoid generic assemblages due to morphological homoplasy. Disjunct patterns were considered doubtful and discussed whenever modern phylogenetic analysis rendered questionable the monophyly of the taxonomic groups.

MATERIAL AND METHODS

All the existing literature on Palaearctic and Afrotropical scarab beetles was used to obtain a detailed information on taxonomy and chorology of the investigated taxa, in order to outline the geographic ranges of genera and species. The bibliographic sources include both the taxonomic revisions of species groups, genera, tribes or subfamilies, and the comprehensive reviews of regional scarab faunas of single countries or broader areas. In the separate sections of this paper, each dedicated to a single taxonomic group, the reader will find the references containing information on the taxa discussed.

The palaeogeographic and palaeoecological scenario of the Cenozoic Era (mainly from Miocene to Pleistocene period) were deduced by several authors e.g.: Axelrod & Raven, 1978; Croizat, 1968; Jürgens N. 1997; La Greca, 1970, 1990; Livingstone, 1975; Moreau, 1952, 1963; Pickfort & Senut, 1999; Quezel P., Barbero M. 1993; van Zinderen Bakker, 1978; Vermeij, G. 1992; Williamson, 1985.

RESULTS

The Mediterranean-southern African disjunct distribution pattern was suggested among few taxonomic groups of scarab beetles, but some of them are currently considered polyphyletic, after modern systematic revisions. In the following review we deal with both monophyletic (true disjunct pattern) and polyphyletic (false disjunct pattern) groups, as they were considered in the literature.

The Pachysomina subtribe, i.e. the flightless species of the genus *Scarabaeus*

The name *Pachysoma* MacLeay, 1821, and *Neopachysoma* Ferreira, 1953 have been used to name a stock of African Scarabaeini characterized by aptery, absence of humeral callus, semicontiguous mesocoxae, and short mesosterna (cf. Ferreira, 1953, 1966). These two genera included several flightless species, all geographically isolated and occurring in pockets of discontinuous populations on coastal sands from Walvis Bay, Namibia, to Cape Town, South Africa. They were traditionally linked to *Neomnematium* Janssens, 1938, with a single species endemic to the desert areas of southern Madagascar, and to *Mnematium* MacLeay, 1821, that included four allopatric species occurring respectively in southern Angola, Somalia, northern Africa (Tunisia and Libya) and some areas of the Near East (viz. Sinaï, Iraq, Syria). The four genera were grouped together to form the subtribe Pachysomina, of the tribe Scarabaeini (Ferreira, 1953, 1966, 1969). Such a taxonomic arrangement led some authors (e.g. Balthasar, 1963) to consider the group as a clear case of Mediterranean-south African disjunct distribution, referable to the third of the distribution patterns defined in the introduction of this paper.

However, a series of systematic evaluations (Holm & Scholtz, 1979; Mostert & Holm, 1982) brought to the conclusions that the characters used to separate these genera and those shared by them were due to convergence for adaptation to dry habitats. For this reason, Holm & Scholtz (1979), proposed to synonymize *Neopachysoma* and *Mnematium* with *Pachysoma*, while Mostert & Holm (1982) reduced the latter to a subgenus of *Scarabaeus* Linnaeus, 1758, and *Neomnematium* to a synonym of the latter. The last revision (Harrison et al., 2003) and phylogenetic analysis (Harrison & Philips, 2003; Forgie et al.,

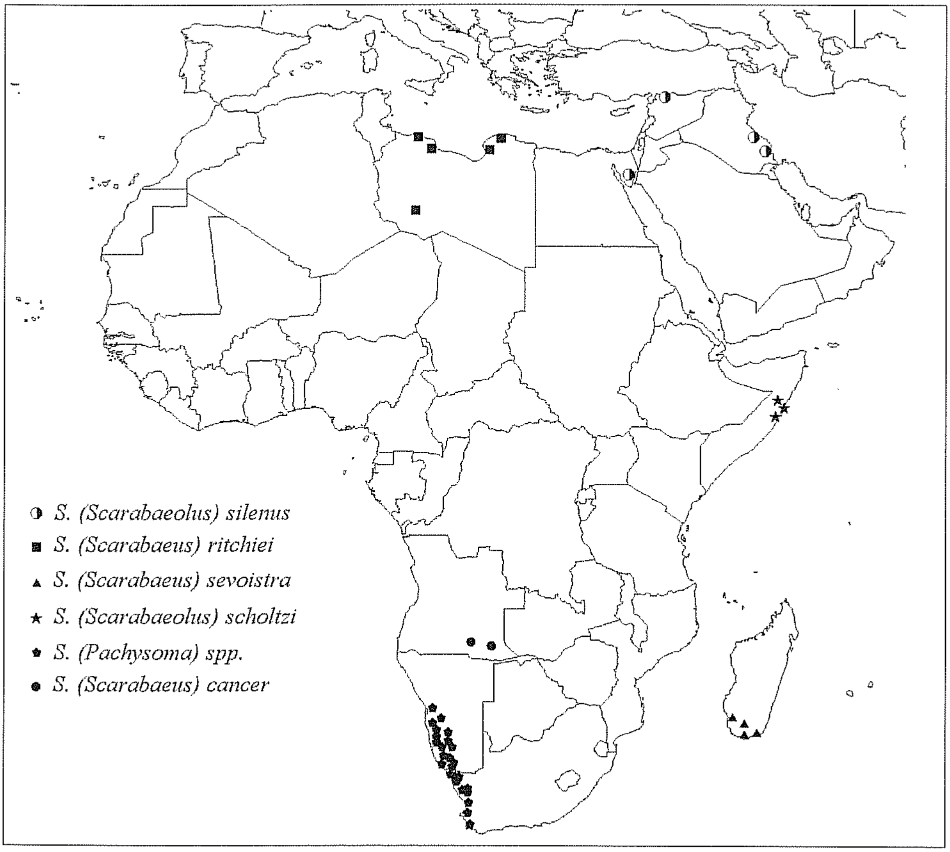

Fig. 1. - A case of false disjunct distribution: distribution of the flightless species of the genus *Scarabaeus* (ex subtribe Pachysomina). Data and taxonomic arrangement from Harrison et al. (2003).

Tab. I. - Taxonomic and chorological account of the old group "Pachysomina", i.e. the flightless species of *Scarabaeus*, according to Harrison et al. (2003). According to Sole et al. (2007) the ancient separation of the clade *Pachysoma* from *Scarabaeus* and its monophyly confirmed by molecular analysis warrant the reinstatement of *Pachysoma* to its former full generic rank.

Checklist of the species of *Scarabaeus (Pachysoma)* Mackleay, 1821: 13 species
Scarabaeus (Pachysoma) aesculapius Olivier, 1789 (S Africa: W Cape)
Scarabaeus (Pachysoma) bennigseni (Felsche, 1907) (Namibia, S Africa: N Cape)
Scarabaeus (Pachysoma) denticollis (Péringuey, 1888) (Namibia) (ex: *Neopachysoma)*
Scarabaeus (Pachysoma) endroedyi Harrison, Scholtz and Chown, 2003 (S Africa: W Cape)
Scarabaeus (Pachysoma) fitzsimonsi (Ferreira, 1953a) (Namibia)
Scarabaeus (Pachysoma) gariepinus (Ferreira, 1953a) (Namibia, S Africa: N Cape)
Scarabaeus (Pachysoma) glentoni Harrison, Scholtz and Chown, 2003 (S Africa: W Cape)
Scarabaeus (Pachysoma) hippocrates (MacLeay, 1821) (S Africa: W Cape)
Scarabaeus (Pachysoma) rodriguesi (Ferreira, 1953a) (Namibia) (ex: *Neopachysoma)*
Scarabaeus (Pachysoma) rotundigenus (Felsche, 1907) (Namibia) (ex: *Neopachysoma)*
Scarabaeus (Pachysoma) schinzi (Fairmaire, 1888) (Namibia)
Scarabaeus (Pachysoma) striatus (Castelnau, 1840) (S Africa: N Cape)
Scarabaeus (Pachysoma) valeflorae (Ferreira, 1953a) (Namibia)

Checklist of the flightless species of *Scarabaeus (Scarabaeolus)* Balthasar, 1965: 2 species
Scarabaeus (Scarabaeolus) scholtzi Mostert and Holm, 1982 (Somalia)
Scarabaeus (Scarabaeolus) silenus (Gray, 1832) (Sinaï, Syria, Iraq) (ex: *Mnematium, Pachysoma)*

Checklist of the flightless species of *Scarabaeus (Scarabaeus)* Linnaeus, 1758: 3 species
Scarabaeus (Scarabaeus) cancer (Arrow 1919) (Angola) (ex: *Mnematium, Pachysoma)*
Scarabaeus (Scarabaeus) ritchiei (MacLeay, 1821) (Tunisia, Lybia) (ex: *Mnematium, Pachysoma)*
Scarabaeus (Scarabaeus) sevoistra (Alluaud, 1902) (Madagascar) (ex: *Neomnematium)*

2006) showed that *Pachysoma* forms a distinct clade within *Scarabaeus* and confirmed its status of subgenus of the latter. Moreover, the same studies showed that there are not close relationships between *Pachysoma* and the other previously recognized genera (*Mnematium* and *Neophachysoma*), because they derived from distinct lineages of the genus *Scarabaeus.* These phylogenetic implications made the subtribe *Pachysomina* meaningless. According to Sole et al. (2005), who combined molecular phylogenetic with geochronological data, the subgenus *Pachysoma* appears to have arisen approximately 2.9 millions years ago, and is relatively young in comparison with the age of the Namib Desert, which dates back to the Miocene (ca. 15 Mya) (Pickfort & Senut, 1999). Moreover, trees obtained from both morphological and molecular analysis by Sole et al. (2007), led us to suggest that monophyly, unique morphology and biology of *Pachysoma* are worth to restore its previous generic level, recovering a sister relationship to *Scarabaeus.* However, as the other flightless species (formerly assigned to *Mnematium,* occurring in North Africa and the Near East), underwent an independent evolution from different lineages of *Scarabaeus,* "Pachysomina" is a polyphyletic group and cannot be used to support the disjunction model investigated here.

The genus *Cheironitis*

According to the current taxonomic arrangement, still untested by a molecular approach, the genus *Cheironitis* Lansberge, 1875 appeared a candidate to support the Mediterranean-southern African model, namely suggesting the fourth of the distribution patterns defined in the introduction of this paper. The genus *Cheironitis* (= *Chironitis*, see Branco & Ziani, 2005) includes 23 species within a wide range that extends from western Europe to central Asia and southern Africa. The distribution patterns of these species can be ordered as follows: East African (from Somalia to Tanzania): 7 species; Southern African: 4 species; Sahelo-Sudanian: 1 species; Sahelo-Sindhian: 1 species; Mediterranean: 3 species; Centralasiatic: 7 species (Tab. II). The genus appears to have two major centres of endemism: the Afrotropical region and western-central Asia. However, taxonomy is still poor and needs a sound revision. Even the Mediterranean and Middle Asiatic species are still questionable (cf. Martin Piera, 1986; Kababov,

Tab. II. - Taxonomic and chorological account of the genus *Cheironitis* Lansberge, 1875.

E African species
C. benningseni Felsche, 1907 (Tanzania, Kenya)
C. dentifemoralis Ferreira, 1976 (Kenya)
C. flabellatus Boucomont, 1923 (Somalia)
C. imitator Balthasar, 1963 (Sudan, Ethiopia, Kenya)
C. muelleri Janssens, 1943 (Ethiopia, Kenya)
C. socotranus Gahan, 1900 (Socotra)
C. viridicans Gillet, 1918 (Somalia)

S African species
C. scabrosus Fabricius, 1776 (S Africa)
C. damarensis Felsche, 1907 (Namibia)
C. hoplosternus Harold, 1868 (S Africa)
C. indicus Lansberge, 1875 (S Africa)

Sahelo-Sudanian species
C. asbenicus Gillet, 1909 (Niger, Chad, Mauretania)

Sahelo-Sindhian species
C. osiridis Janssens, 1943 (Pakistan, Arabia, Egypt, Sudan, Chad)

Mediterranean species
C. furcifer Rossi, 1792 (Mediterranean)
C. hungaricus Herbst, 1789 (SE European)
C. irroratus Rossi, 1790 (W Mediterranean)

Middle Asiatic species
C. arrowi Janssens, 1937 (Pakistan, India, Afghanistan, Arabia)
C. candezei Lansberge, 1875 (Irak, Turkmenia, Iran)
C. haroldi Ballion, 1870 (Caucasia, Transcaspia,Turkestan, Iran, Afghanistan, Cyprus)
C. moeris Pallas, 1781 (Southeast Ukraine, Turkestan, Turkmenistan)
C. pamphilus Menetries, 1849 (Siria-Mongolia)
C. phoebus Reitter, 1892 (E Ukraina- Turkestan)
C. sterculius Ballion, 1870 (Turkestan)

2000, 2006). For instance, a recent review of this genus in Russia and neighbouring countries (Kabakov, 2000) brought to synonymyze two Palearctic species. As for the Afrotropical species, the taxonomic arrangement of the whole tribe Onitini is very weak and confused, notwithstanding the revisions by Janssens (1937) and Ferreira (1978). The validity of the genus *Pseudochironitis* Ferreira, 1977 should be checked, as well as the identity of some African species of the genus *Onitis* Fabricius, 1798, that could be moved to *Cheironitis* after a careful investigation. Unluckily, many species of Onitini are rare or localized, often with a restricted phenology. Probably, a detailed morphological revision of the whole tribe could change the current scenario enriching the synonymy of *Cheironitis* and adding new species to the latter. A combined morphological-cladistic and molecular approach could resolve the phylogeny of this genus and verify if a new taxonomic arrangement will be adequate to support the disjunction model, at least for some eventually emerging species groups.

The genus *Bordatius*

The genus *Bordatius* was established by Pittino and Mariani (1986) during a comprehensive revision of some genera of Old World Rhyssemini, a tribe of sand dwelling scarab beetles of the subfamily Aphodiinae. The genus includes only four species (Tab. III) and was defined basing on the following characters, whose synapomorphy is questionable: flightless due to microptery, short and strongly convex body, short metasternum with reduced sculpture, very small scutellum, coalescent elytra, slender hind femur and distinct vestiges of oblique ridges on both middle and hind tibia (Pittino, & Mariani, 1986; Pittino 1996).

The members of this genus are very rare and localized: all the species are known only from the type specimens. A cladistic approach, based on both morphological and molecular data, should be applied in order to test the phylogenetic relationships between the three southern African species and the unique moroccan member of the genus. If monophyly will be ascertained, this genus could represent the most evident example of the Mediterranean-southern African model among the scarab beetles.

Tab. III. - Taxonomic and chorological account of the genus *Bordatius* Pittino & Mariani, 1986.

N African species
Bordatius tingitanus Pittino & Mariani, 1986 (Morocco)

S African species
Bordatius australis Pittino & Mariani, 1986 (South Africa: Transkei)
Bordatius capensis Pittino & Mariani, 1986 (South Africa: Cape)
Bordatius muellerae Pittino, 1996 (South Africa: Cape)

The genera *Ammoecius* and *Ammoecioides*

For a long time, *Ammoecius* Mulsant, 1842, was considered one of the most easily recognizable 'genus groups' within *Aphodius* Illiger, 1798. In the old classification proposed by Mulsant (1842), *Ammoecius* was the unique representative of the taxon named 'Ammoeciates' one of the three major groups recognized by this author within Aphodiinae. The species belonging to this taxonomic group show a convex body, black colour and a peculiar shape of clypeus. According to classic taxonomic arrangement, based on morphology, 38 species have been assigned to *Ammoecius*, most ranging from Mediterranean countries, but few localized in southern Africa and North America (cf. Dellacasa, 1987). In the last decades, several taxonomic changes as the description of new species in southern and eastern Africa, and the establishment of several synonyms, in the framework of a morphological approach focused on phylogenetic relationships, led some authors (Bordat, 1985, 1990, 1999; Dellacasa et al., 2002) to redefine and split the genus as follows: 1) the Palearctic species and few Southern African species remained to represent the genus *Ammoecius;* 2) a cluster of African species was included in a genus apart, *Ammoecioides* Bordat, 1999; 3) the Nearctic species were removed from the genus and considered *incerta sedis* (Dellacasa et al., 2002). The genus *Ammoecioides* consists of ten species, almost all ranging south of the Fortieth Parallel, from Malawi to the Cape region; only one species reaches northwards Ethiopia but is very rare and localized. On the contrary, the 21 species of the redefined genus *Ammoecius* show four distribution patterns (Tab. IV):

1) W Mediterranean (mainly from north-western Africa): 10 species;

2) E-Mediterranean with extension to Middle East (from Turkey to Iran): 5 species;

3) Southern African (from Namaqualand to the former Transvaal): 4 species;

4) Sibero-European (widespread): 1 species;

5) Eastern Palaearctic (endemic to Japan): 1 species.

Apart from the strange case of *A. yamato* Nakane, 1960, from Japan, and *A. brevis* Erichson, 1848, which shows a widespread Palearctic range, the other species give the genus a typical Mediterranean-southern African distribution pattern. Only *A. brevis* shows a widespread Palearctic range. The phylogenetic relationships within this genus and with *Ammoecioides* need to be tested by a molecular approach, widened to all the Aphodiini. It will be an arduous task because of either the high number of species of this tribe or the rareness of these southern African species.

Tab. IV. - Taxonomic and chorological account of the related genera *Ammoecius* Mulsant, 1842, and *Ammoecioides* Bordat, 1999.

***Ammoecius* Mulsant, 1842 (21 species)**

W Mediterranean (10 species)
Ammoecius amplicollis Peyerimhoff, 1949 (Morocco)
Ammoecius dentatus Schmidt, 1908 (Spain, Portugal, Morocco)
Ammoecius dogueti Baraud, 1980 (Algeria)
Ammoecius elevatus Olivier, 1789 (South-western Europe: Portugal, Spain, southern France, northwestern Italy (western Liguria), Mediterranean Africa: Morocco, Algeria, Tunisia, Libya)
Ammoecius felscheanus Reitter, 1904 (Algeria)
Ammoecius franzi Petrovitz, 1964 (Morocco)
Ammoecius frigidus Brisout, 1866 (Spain, Portugal, Morocco?)
Ammoecius lusitanicus Erichson, 1848 (Spain, Portugal, Morocco?)
Ammoecius numidicus Mulsant, 1851 (Morocco, Algeria, Tunisia)
Ammoecius rugifrons Aube, 1850 (Algeria, Tunisia, Sicily, Sardinia)

E Mediterranean (including their relatives of the Near East) (5 species)
Ammoecius eli Petrovitz, 1961 (Irak)
Ammoecius meurguesae Clement, 1975 (Iran, Azerbaijan)
Ammoecius muchei Petrovitz, 1963 (Turkey)
Ammoecius naviauxi Baraud, 1971 (Syria)
Ammoecius satanas Carpaneto, 1976 (Turkey)

S African (4 species)
Ammoecius incultus Petrovitz, 1961 (South Africa)
Ammoecius lugubris Boheman, 1857 (South Africa)
Ammoecius mimus Peringuey, 1901 (South Africa)
Ammoecius terminatus Harold, 1869 (South Africa)

E Palearctic (1 species)
Ammoecius yamato Nakane, 1960 (Japan)

Widespread Palearctic (1 species)
Ammoecius brevis Erichson, 1848 (Europe: northwards up to Sweden, south from Spain to Georgia, Turkmenistan, Mongolia, Siberia: Irkutsk region)

***Ammoecioides* Bordat, 1999 (10 species)**

Ammoecioides adventicius Bordat, 1999 (South Africa)
Ammoecioides davisianus Bordat, 1999 (South Africa)
Ammoecioides facetus Bordat, 1999 (South Africa)
Ammoecioides insidiosus Bordat, 1999 (South Africa)
Ammoecioides kovacsi Bordat, 1990 (Ethiopia, Kenya, Malawi)
Ammoecioides mulanje Bordat, 1985 (Malawi, Transvaal)
Ammoecioides nyika Bordat, 1999 (Malawi, South Africa)
Ammoecioides sparsepunctatus Petrovitz, 1964 (South Africa)
Ammoecioides spectabilis Péringuey, 1901 (South Africa)
Ammoecioides uitsoekensis Bordat, 1999 (South Africa)

The *Omaloplia* and *Pleophylla* clade

In the last years, the research activity of Ahrens and colleagues (Ahrens, 2004, 2006, 2007; Rossner & Ahrens, 2004; Ahrens & Vogler, 2008) began to enlighten the phylogenetic relationships within the tribe Sericini (Scarabaeidae: Melolonthinae) and made it suitable for phylogeographical speculations. A Mediterranean-southern African distribution pattern may be observed in the clade formed by the genera *Omaloplia* Schönherr, 1817 (Western Palaearctic) and *Pleophylla* Erichson, 1847 (southern African) which have been found to be sister groups (Ahrens, unpublished data) based on a preliminary analysis of molecular and morphological data. The first genus is widespread in Europe and central Asia, while the second one is restricted to southern Africa (from Natal to Cape), with a few single occurrences in the east African mountain arc. The sister relationships between these two genera need a confirmation from an analysis with a wider taxon sampling to establish if the pattern represents a case of disjunct distribution or a gap of knowledge.

CONCLUSIONS

The scarab beetles did not provide study cases suitable to reflect a disjunct Mediterranean-southern African distribution pattern. Among the four groups analyzed, we found the following case histories:

1) a group previously considered as a proper examples of the model (the ex-subtribe Pachysomina), whose biogeographic significance was recently reinterpreted on the ground of modern taxonomic revision and thus represents an artefact of incorrect taxonomy (false disjunction);

2) a seemingly copybook case of the model (*Bordatius*) which however was never tested by a phylogenetic analysis (it deals with a recently defined genus, scarcely investigated, including very uncommon species whose geographic range could be still insufficiently known);

3) a widespread taxonomic group (*Cheironitis*) that still needs a phylogenetic revision based on either morphological or molecular approaches (some Mediterranean representatives of this genus may be related to some southern African ones but this hypothesis needs a confirmation in the frame of a proper phylogenetic analysis with a subgeneric subdivision);

4) two groups that roughly fit the model (*Ammoecius* and the cluster *Omaloplia/Phleophylla*) but include some representatives widely spread into Eurasia (e.g. *Ammoecius brevis* and *Omaloplia nigromarginata*). In any case, both these groups need a sound phylogenetic analysis.

Therefore, the occurrence of a Mediterranean-southern African disjunct distribution pattern in the scarab beetles is in major part still limited to phenotypical similarity rather than true phylogenetic relationships (except the case of Sericini). We conclude that the support for any biogeographical speculations is low and needs further phylogenetic work; nevertheless, more cases of disjuction of clades may be discovered from future cladistic analyses.

ACKNOWLEDGEMENTS

I am grateful to Marco A. Bologna (Department of Biology, University "Roma Tre") who was the main coordinator of the project "Zoogeography of Mediterranean-southern African disjunct distributions by a multimethod approach" PRIN (Research Project of National Interest) 2004-2006. Dirk Ahrens gave a sound contribution with data concerning Sericini, and a critical review of the first version of this paper. Many thanks are due to the colleagues Alberto Ballerio, Giovanni and Marco Dellacasa, Riccardo Pittino, for useful information and suggestions. I am also indebted to Pierluigi Bombi and Monica Pitzalis, who help me to arrange the map figures.

REFERENCES

Ahrens D. 2004 - Monographie der Sericini des Himalaya (Coleoptera: Scarabaeidae). Deutsches Entomologisches Institut (DEI), Leibniz- Zentrum für Agrarlandschafts- und Landnutzungsforschung (ZALF) e.V.

Ahrens D. 2006 - The phylogeny of Sericini and their position within the Scarabaeidae based on morphological characters (Coleoptera: Scarabaeidae). *Syst. Entomol.*, **31** (1): 113-144.

Ahrens D. 2007 - Type species designations of Afrotropical Ablaberini and Sericini genera (Coleoptera: Scarabaeidae: Melolonthinae). Zootaxa, **1496**: 53-62.

Axelrod D., Raven P. 1978 - Late cretaceous and tertiary vegetation history of Africa. In: Werger M. J. (ed.), Biogeography and Ecology of Southern Africa. Junk, The Hague: 77-130.

Balthasar V. 1963 - Monographie der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia), 1. Verlag der Tschechoslowakischen Akademie der Wissenschaft, Prague.

Branco T., Ziani S. 2005 - *Cheironitis* Lansberge, 1875 - its correct spelling and validity (Coleoptera, Scarabaeidae). Bol. Soc. Entomol. Aragon., **37**: 267-272.

Croizat L. 1968 - Introduction raisonnée à la Biogéographie de l'Afrique. Mem. Soc. Broteriana, **20**: 7-451.

Dellacasa G. 1988 - Contribution to a world-wide catalogue of Aegialiidae, Aphodiidae, Aulonocnemidae, Termitotrogidae. Mem. Soc. Entomol. Ital., **66**: 1-455.

Dellacasa G., Bordat P., Dellacasa M. 2001 - A revisional essay of world genus-group taxa of Aphodiinae. Mem. Soc. Entomol. Ital., **79**: 1-482.

de Winter B. 1971 - Floristic relationships between the northern and southern arid areas of Africa. Mitt. Bot. Staatssam. München, **10**: 424-37.

Endrödy-Younga S. 1978 - Coleoptera. In: Werker M. J. (ed.), Biogeography and Ecology of Southern Africa. Junk, The Hague: 797-821.

Ferreira M.C. 1953 - Monografia dos escarabídeos da Africa do Sul. Tribo-Scarabaeini. I Parte, Sub-tribo Pachysomides. Bol. Soc. Estudos Prov. Moçambique, **23**: 1-85.

Ferreira M. C. 1966 - Os Escarabídeos de la sub-regiao natural de África do Sul. II. Chave para determinacao das especies dos generos *Pachysoma* M'Leay e *Neopachysoma* Ferreira da subtribo Pachysomina (tribo Scarabaeini). Mem. Inst., Invest. Cient. Moçambique, 8(A): 53-60.

Ferreira M. C. 1969 - Os Escarabídeos de África (Sul do Sáara). Rev. Entomol. Moçambique, **11**: 5-1088.

Ferreira M. C. 1978 - The genus *Onitis* F. of Africa south of the Sahara (Scarabaeidae, Coleoptera). Mem. Nasion. Mus. Bloemfontein, **10**: 1-410.

Forgie S. A., Philips T. K., Scholtz C. H. 2005 - Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae). Syst. Entomol., **30**: 60-96.

Harrison J. G. du , Philips T.K. 2003 - Phylogeny of *Scarabaeus* (*Pachysoma* MacLeay) stat.n. and related flightless Scarabaeini (Scarabaeidae: Scarabaeinae). Ann. Transv. Mus., **40**: 47-71.

Harrison J.G. du, Scholtz C.H., Chown S.L. 2003 - A revision of the endemic south-western African dung beetle subgenus *Scarabaeus (Pachysoma)* Macleay, including notes on other flightless Scarabaeini (Scarabaeidae: Scarabaeinae). J. Nat. Hist., **37**: 305-355.

Holm E. 1978 - Monograph of the genus *Acmaeodera* Eschscholtz (Coleoptera, Buprestidae) of Africa south of Sahara. Entomol. Mem. Dep. Agric. Tech. Serv. Rep. S. Africa, **47**: 1-210.

Holm E. 1979 - Revision of the genera of the tribe Julodini (Coleoptera: Buprestidae). J. Entomol. Soc. South Africa, **42**: 89-114.

Holm E., Scholtz C.H. 1979 - A revision of the genus *Pachysoma* M'Leay with an evaluation of the subtribe Pachysomina Ferreira and its genera (Coleoptera: Scarabaeidae). J. Entomol. Soc. South Africa, **42**: 225-244.

Janssens A. 1937 - Revision des Onitides. Mem. Mus. R. Hist. Natur. Belg., (2) **11**: 1-200.

Janssens A. 1938 - Scarabaeini, Coleoptera, Lamellicornia, Fam. Scarabaeidae. Exploration du Parc National Albert, Mission G.F. De Witte, **21**: 65-75.

Janssens A. 1940 - Monographie des *Scarabaeus* et genres voisins. Mem. Mus. R. Hist. Natur. Belg, **2**: 1-84.

Jürgens N. 1997 - Floristic biodiversity and history of African arid regions. Biodiversity and Conservation, **6**: 495-514.

Kabakov O. N. 2000 - Revision of the Scarabaeid Genus *Chironitis* Lansb. (Coleoptera, Scarabaeidae) from Russia and Neighbouring Countries. Entomol. Rev., **79**: 625-642 (in Russian).

Kabakov O. N. 2006 - The lamellicorn beetle subfamily Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) in the fauna of Russia and adjacent countries (Plastinchatousye zhuki podsemeistva Scarabaeinae fauny Rossii i sopredel'nykh stran). KMK Sci. Press, Moskow (in Russian).

La Greca M. 1970 - Considérations sur le peuplement animal terrestre de l'Afrique. C. R. Soc. Biogéogr., **409**: 5-33.

La Greca M. 1990 - Considerazioni sul popolamento animale dell'Africa Orientale. Biogeographia, (n.s.) **14**: 541-578.

Livingstone D. 1975 - Late Quaternary climatic change in Africa. Ann. Rev. Ecol. System., **6**: 249-280.

Martin Piera F. 1987 - Review of the Genus *Chironitis* Lansberge, 1875. I: taxonomy, phylogeny and zoogeography of the Palearctic species. (Col. Scarabaeoidea, Onitini). Ent. Arb. Mus. Frey, **35-36**: 203-245.

Mostert L.E., Holm E. 1982 - Notes on the flightless Scarabaeina (Coleoptera: Scarabaeidae) with a description of a new species. Cimbebasia (A), **5**: 273-284.

Mostert L. E., Scholtz C. H. 1986 - Systematics of the subtribe Scarabaeinae (Coleoptera: Scarabaeidae). Entomol. Mem. Dep. Agric. Water Suippl. Rep. S. Africa , **65**: 1-25.

Müller P. 1974 - Aspects of zoogeography. Junk, The Hague.

Pickford M., Senut, B. 1999 - Geology and palaeobiology of the central and southern Namib Desert, southwestern Africa. 1. Mem. Geol. Surv. Namibia, **18**: 1-155.

Pittino R., Mariani G. 1986 - A revision of the Old World species of the genus *Diastictus* Muls. and its allies. Giorn. Ital. Entomol., **3**: 1-165.

Pittino R., 1996 - A new *Bordatius* Pittino and Mariani from South Africa (Coleoptera Aphodiidae Psammodiinae). Giorn. Ital. Entomol , **8**: 69-70.

Ratcliffe, B. C. , M. L. Jameson M. L. 2004 - The revised classification for Scarabaeoidea: what the hell is going on? Scarabs (University of Nebraska State Museum), **15**: 3-10.

Rossner E., Ahrens D. 2004 - Taxonomie und Chorologie der Gattung *Omaloplia* (Coleoptera: Scarabaeidae: Sericini). Deutsches Entomologisches Institut (DEI), Leibniz-Zentrum für Agrarlandschafts- und Landnutzungsforschung (ZALF) e.V.

Sole C.L., Scholtz C. H., Bastos A. D. S. 2005 - Phylogeography of the Namib Desert dung beetles *Scarabaeus (Pachysoma)* MacLeay (Coleoptera: Scarabaeidae). J. Biogeogr. **32**: 75-84.

Sole C. L., Bastos A. D. S., Scholtz C. H. 2007 - Do individual and combined data analyses of molecules and morphology reveal the generic status of '*Pachysoma*' MacLeay (Coleoptera: Scarabaeidae)? Insect Syst. Evol., **38**: 311-330.

van Zinderen Bakker E. 1978 - Quaternary vegetation changes in Southern Africa. In: Werger M. J. (ed.), Biogeography and Ecology of Southern Africa. Junk, The Hague: 131-43.

Vermeij G. 1992 - Trans-equatorial connections between biotas in the temperate Atlantic. Mar. Biol., **112**: 343-348.

White F. 1983 - The vegetation of Africa. Unesco, Paris.

Williamson P. G. 1985 - Evidence for an early Plio-Pleistocene rainforest expansion in East Africa. Nature, **315**: 487-489.