

Examples of disjunct distributions between Mediterranean and southern or eastern Africa in Meloidae (Coleoptera, Tenebrionoidea)

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SUMMARY

In this paper some cases of distribution in Coleoptera Meloidae, possibly referable to the distributional "Mediterranean-southern African disjunct model", are examined and discussed. At least four genera, two belonging to the subfamily Meloinae, tribe Mylabrini (*Actenodia* Laporte de Castelnau, 1840 and *Ceroctis* Marseul, 1870), and two to the subfamily Nemognathinae, tribe Nemognathini (*Sitaris* Latreille, 1802 and *Stenoria* Mulsant, 1857), have ranges which include both the Mediterranean-Saharan area and eastern and southern Africa. Other examples, briefly examined, concern taxa of Meloinae or Nemognathinae which are primarily Mediterranean or Saharan, with isolated subranges also in the eastern Africa. Two main considerations seem evident from this analysis: 1) a distributional disjunct model with only Mediterranean and South African related species does not exist among Meloidae, but at most genera which have the greatest diversity in these two areas and relict species in eastern Africa; 2) the type of disjunct distribution observed in some genera of Meloidae seems referable to convergent biogeographical phenomena more than a late, single vicariance event.

INTRODUCTION

Meloidae is a family of Coleoptera Tenebrionoidea including about 3,000 species, belonging to approximately 130 genera (Bologna, 1991; Pinto and Bologna, 1999; Bologna and Pinto, 2001; Bologna, unpubl.). The biological and pharmacological literature widely treated these beetles, respectively because of their hypermetabolic larval development, which includes parasitic habits, and their production of cantharidin, a natural terpenoid used in the popular pharmacy, particularly as aphrodisiac (see Bologna, 1991 for a review of both aspects).

The taxonomy of Meloidae genera and their distribution were recently reviewed by Pinto and Bologna (1999) and by Bologna and Pinto (2001) as concerns the New World and the Old World respectively. The Australasian

taxa are still under study (Bologna et al., unpubl.). The phylogeny and classification of this family were studied by Bologna and Pinto (2001) using morphological and biological characters, and Bologna et al. (2008b) by molecular and combined characters.

In this framework, the biogeography of the whole family at a World scale was briefly attempted only by Bologna (1991). Faunistical and biogeographical analyses at a regional scale were performed in different geographical areas, particularly of Palaearctic and Afrotropical Regions (e.g., Afghanistan: Kaszab, 1973; Arabian Peninsula: Kaszab, 1983; Bologna and Turco, 2007; Greece: Bologna and Marangoni, 1986; Bologna, 1994; Italy: Bologna, 1991; Levant: Bologna, 1988; Libya: Bologna, in press; Mauritania: Bologna, 1985; Namibia: Bologna et al., unpubl.; Somalia: Bologna, 1990).

Instead, this beetle group was used to test general biogeographical models only in few cases. At a local scale the relict condition of Apennine populations of *Mylabris* species, due to glacial periods, was examined by allozymes or molecular markers (Bologna et al., 1988; Ketmayer et al., in press); moreover, the extraordinary process of endemism of several meloid taxa in the south-western Africa was tested by a multidisciplinary method (Pitzalis, 2007; Pitzalis and Bologna, 2008; unpubl.). At a world scale, a scenario of the biogeographical history of the entire family was depicted by a molecular clock analysis by Bologna et al. (2008b). This study demonstrated the Gondwanan origin of the family Meloidae and several late vicariance events and more recent dispersal phenomena, which explain the present distribution of subfamilies and tribes.

Aim of this paper is to analyse some cases of distribution among the subfamilies Meloinae and Nemognathinae, which seem to reflect a biogeographical disjunct model, possibly referable to the distributional “Mediterranean-southern African disjunct model”, as defined in this volume (Bologna et al., 2008c). At least four genera, two belonging to the subfamily Meloinae, tribe Mylabrini (*Actenodia* Laporte de Castelnau, 1840; *Ceroctis* Marseul, 1870), and two to the subfamily Nemognathinae, tribe Nemognathini (*Sitaris* Latreille, 1802; *Stenoria* Mulsant, 1857), have ranges which include both the Mediterranean-Saharan area as well as eastern and southern Africa, but never central or western African countries.

Other examples, briefly examined, concern taxa of Meloinae or Nemognathinae, which are primarily Mediterranean or Saharan, with isolated distribution also in the eastern Africa. These cases could represent events of shorter dispersal along the same intermediate zones involved in the previous cases. The examined examples concern species of the following taxa: *Alosimus* Mulsant, 1857, *Cabalia* Mulsant and Rey, 1858 (both tribe Lyttini), the sister genera *Diaphorocera* Heyden, 1863 and *Somalarthrocera* Turco and

Bologna, 2008 (tribe Cerocomini), *Epicauta* Redtenbacher, 1845, (tribe Epicautini), *Meloe* Linnaeus, 1758, subgenus *Eurymeloe* Reitter, 1911 (tribe Meloini), and *Leptopalpus* Guérin de Méneville, 1844 (tribe Nemognathini).

RESULTS

I. Taxa with disjunct ranges, Mediterranean and southern Africa, with relict species in eastern Africa

(a) The genus *Actenodia* Laporte de Castelnau, 1840

The mylabrine genus *Actenodia* was recently revised by Bologna et al. (2008a). Molecular studies (Bologna et al., 2005) support the monophyly of the genus, and identify as sister group the genus *Mimesthes* Marseul, 1872, endemic to south-western Africa (Bologna, 2000). That study (Bologna et al., 2008a) provided evidence for the existence of two very distinct lineages, one Afrotropical and one Palearctic, supported by adult, larval and molecular characters. Strong differences exist in the larval features of these lineages, with the least derived first instar larva of *Actenodia*, *A. chrysomelina* (Erichson, 1843), belonging to the Afrotropical group, suggesting an Afrotropical origin of the genus.

Actenodia includes 18 species, 16 of which are clearly referable to the Afrotropical and Palearctic lineages. Two species, one in each biogeographical region [*A. mirabilis* Kaszab, 1952, from Namaqualand, and *A. perfuga* (Dvorak, 1993) from Syria], remain phylogenetically unresolved and very isolated. The Afrotropical clade resulted well explained in all analyses, while relationships inside of the Palearctic lineage are more controversial, but two main groups of species were defined. Ranges of distribution of these groups of species are summarized in Fig. 1. The Afrotropical lineage includes the following three groups of species, widely distributed in southern Africa with isolated elements in the eastern regions of the continent (Fig. 1). (a) The group of *A. chrysomelina*, with five species: *A. carpanetoi* Bologna and Di Giulio, 2008 from a single locality of central Mozambique; *A. cerrutii* Bologna, 1978, endemic to a small zone of eastern Ethiopia; *A. chrysomelina*, widely distributed from the Angola, Namibia, Botswana, north-eastern South Africa and south Mozambique; *A. luteofasciata* Pic, 1929 from few localities of southern Ethiopia, central Somalia and eastern Kenya; *A. unimaculata* Pic, 1908 with a similar distribution including few localities of central Somalia, Kenya and Tanzania. (b) The group of *A. guttata* Laporte de Castelnau, 1840, with two species: *A. curtula* Fähræus, 1870 from south Botswana and eastern South Africa; *A. guttata* from southern South Africa. (c) The monotypic group of *A. confluens* (Reiche, 1866), distributed in eastern Bulgaria and European Turkey,

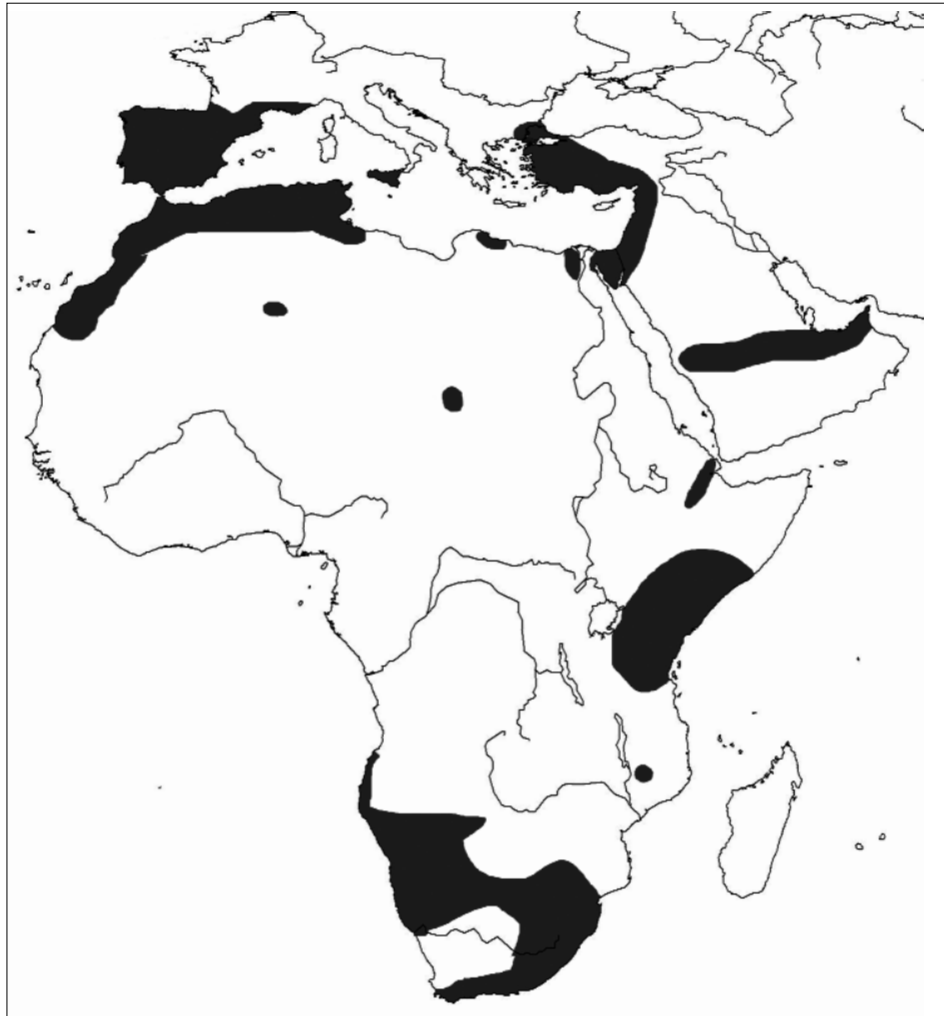


Fig. 1 - Distribution map of the genus *Actenodia*.

western Anatolia, and perhaps also in the Levant south to Sinai peninsula. This group represents an interesting possible isolated example of dispersal from eastern Africa to eastern Mediterranean of this lineage.

As previously indicated, *A. mirabilis* from the Namaqualand (south-western Namibia, north-western South Africa) appears to be extremely different, and possibly represents another extremely specialized lineage evolved in the desert habitat of north-western Namaqualand and southern Namib.

The Palearctic lineage includes two groups of species, phenetically well distinct, but phylogenetically very close, one of which, the Saharo-Arabian, well

supported also by cladistic analyses (Fig. 1). (d) The Mediterranean group of *A. distincta* (Chevrolat, 1838) includes four species: *A. billbergi* (Gyllenhal, 1817) from the Iberian Peninsula, southern France and western Liguria (probably extinct); *A. distincta* from Maghreb and Sicily, with uncertain populations in Andalusia; *A. peyroni* (Reiche, 1866) distributed along the Mediterranean countries from southern Turkey to Levant, northern Egypt and Cyrenaica; *A. septempunctata* (Baudi di Selve, 1878), distributed in the western pre-Saharan regions from Morocco to Tunisia. (e) The Saharo-Arabian group of *A. denticulata* (Marseul, 1871) includes four species: *A. denticulata*, endemic to the Arabian Peninsula; *A. lata* (Reiche, 1866), endemic to the northern Egypt; *A. mateui* Pardo Alcaide, 1966, endemic to the Ennedi Massif, central Sahara; *A. suturifera* (Pic, 1896), distributed in the northern-west Sahara, from Morocco to Tripolitania.

As indicated, the Syrian species *A. perfuga* remains cladistically unresolved and also its inclusion in the genus *Actenodia* is uncertain.

The distribution of *Actenodia* was deeply analysed by Bologna et al. (2008a). It clearly refers to the biogeographical model discussed in this volume (Bologna et al., 2008b). According to phylogenetic evidences (both morphological and molecular), we infer an old separation between the Afrotropical and Palearctic lineages. Three different hypotheses can be formulated to interpret the disjunction of the generic range. (1) A late Tertiary vicariance event between northern Africa and sub-Saharan regions as a result of climatic changes, which fragmented an earlier *Actenodia* range. (2) The origin of this genus in Africa with dispersal to the Saharo-Mediterranean area along a savannah corridor, which extended throughout eastern Africa during the Pliocene and Pleistocene, as a result of the repeated expansion of tropical forests and deserts. This model was proposed to explain present-day distributions of several organisms and massive extinctions in the interposed tropical and subtropical African areas (e.g. Axelrod and Raven, 1978; La Greca, 1970). Moreover, there is some evidence of a middle and late Tertiary dispersal of southern African karoooid beetles (Osella et al., 1998), which could represent vicariant relicts of an ancient continuous biome extending throughout Africa, when a more or less continuous vegetation of savannah and sclerophyll thorn scrub existed in most of the Saharan region until the late Pliocene. (3) The origin of *Actenodia* in the Mediterranean and the subsequent dispersal from the north to the south. This hypothesis could be supported by evidence showing that Saharo-Mediterranean vegetation existed along the coasts of eastern and southern Africa during the dry periods of the late Tertiary and Quaternary, and by fossil pollens and relict taxa, particularly amongst plants (e.g. Axelrod and Raven, 1978; Van Zinderen Bakker, 1978; Werger, 1983; White, 1983; Quezel and Barbero, 1993; Jürgens, 1997).

The analysis within the main groups of *Actenodia* is consistent with separate radiations in the late Miocene-Pliocene, after their previous splitting, which could be explained according to palaeoecological information. (1) In the Palaearctic region, the Saharo-Arabian group (*A. denticulata* group) is homogeneous, even though it is composed of species isolated in distinct Saharan districts, probably as a result of the repetitive and cyclic pulsations of the desert versus savannah and steppe biomes during the Pliocene and Pleistocene. The Mediterranean group (*A. distincta* group) is more heterogeneous, denoting a possible older origin, and includes three species adapted to more or less xeric maquis habitat and one to semi-desert or desert ecosystem. (2) In the Afrotropical region, the genus radiated in two distinct groups: the eastern-southern African group (*A. chrysomelina* group) with species endemic to isolated east African areas, sometimes very restricted, and a single southern African species, widely distributed through savannah ecosystems, which is related to a species endemic to Ethiopia. This group is very distinct from the second group (*A. guttata* group), which is strictly South African and seems to be adapted to Mediterranean ecosystems or to xeric savannahs.

If the inclusion of the monotypic *A. mirabilis* group in the genus *Actenodia* will be confirmed, the biogeographical scenario would indicate a possible wider ecological radiation of the genus in southern Africa, explainable by the older colonization of this area by the ancestor of the Afrotropical lineage, as in the Tenebrionidae tribe Molurini (Endrödy-Younga, 1978), or by a more recent radiation related to the mixture of desert and savannah ecosystems occurring in this region.

The information gained from molecular clock analysis is questionable because the time of separation appears very long (Bologna et al., 2008b). The hypothesis of an ancient Miocene distribution of the genus *Actenodia* through the old southern and eastern African lands to North Africa and Arabia is congruent with the time of separation between the Afrotropical and Palaearctic groups obtained by our molecular clock (about 18 Mya). This dating explains the high level of distinction. This main separation could be determined by an old phenomenon of desertification of the Saharo-Arabian area; similar events have repeatedly occurred since the Miocene, through the Pliocene and Pleistocene to the Holocene. The separate radiations of each *Actenodia* lineage started after this old event, as supported by the molecular clock hypothesis. For example, the relatively old separation between the Afrotropical species *A. guttata* and *A. chrysomelina*, belonging to two well-separated groups, is congruent with a time of separation of over 6 Mya. Similar high values existing amongst the Palaearctic species are congruent with the heterogeneity of this lineage. The colonization of the north Mediterranean lands could be hypothesized after distinct dispersal events, according to the palaeogeography of this

area (e.g. Meulenkamp and Sissingh, 2003): the Tortonian connection between the Arabian and the Anatolian lands (about 8 Mya), the Messinian 'salinity crisis' (ca. 7 Mya) and the land connection between the Maghreb and the Iberian Peninsula (c. 6-5 Mya).

(b) The genus *Ceroctis* Marseul, 1870

This taxon, belonging to the tribe Mylabrini, was described as a subgenus of *Mylabris* Fabricius, 1775, and afterwards was distinct in the main literature (e.g. Borchmann, 1917; MacSwain, 1956; Kaszab, 1969; Bologna, 1991; Selander, 1991; Bologna and Pinto, 2001, 2002). Recent molecular analyses (Bologna et al., 2005, 2008b), as well as morphological evidences on both adults (Bologna and Pinto, 2002) and larvae (Di Giulio and Bologna, 2007), supported its inclusion, as a subgenus, in the speciose and heterogeneous genus *Hycleus* Latreille, 1829. Their closer relationships were singled out with the assumed genus *Paractenodia* Péringuey, 1909, endemic to the south-western Africa, which also resulted part of *Hycleus*. Waiting for the revision of this last taxon, we prefer to maintain *Ceroctis* as a distinct genus.

Ceroctis was never revised, but its study is in preparation (Bologna, unpubl.). Moreover, its faunistics is well outlined after the examination of several museum collections, and its taxonomy is clarified in several aspects. The *Ceroctis* range (Fig. 2) parallels that of *Actenodia*, but with a minor distribution in the Palaearctic Region (northern Africa, southern Levant, Saudi Arabia), and an extension to central Africa. The phylogenetic relationships among species are still not clarified, but some groups of species seem supported by phenetic similarities and larval features.

The taxon is primarily Afrotropical, but one monotypic group of species is Mediterranean. It includes *C. trizonata* (Reiche, 1866) (to which we refer temporarily also *C. coronata* Marseul, 1872), distributed in xeric Mediterranean or pre-Saharan areas from western Sahara and Morocco through almost the whole northern Africa (records from Algeria, Tunisia, Tripolitania, Egypt) east to Sinai, Negev and the Jordan Valley.

The remaining 57 described taxa (the validity of some of which needs confirmation) are distributed in the eastern sub-Saharan Africa and in the Arabian Peninsula. According to Kaszab (1983), both the Yemenite and Arabian species (*C. yerburyi* Gahan, 1896 and *C. wittmeri* Kaszab, 1983) belong to different Afrotropical groups of species. The northernmost point of the Afrotropical distribution of the genus is represented by the Ogaden and Djibouti, and central Arabian Peninsula, while the genus is not present in central Ethiopia and in the whole Sahel.

Some groups of species include species from both eastern and southern Africa. For example: (a) the group of *C. aurantiaca* (Fairmaire, 1885) includes 3 species



Fig. 2 - Distribution map of the genus *Ceroctis*.

distributed in Ethiopia, Somalia, Kenya and Tanzania [*C. aurantiaca*, *C. paolii* (Pardo Alcaide, 1958), *C. rufimembris* Thomas, 1897], and one or two in southern Africa [*C. bohemanii* (Marseul, 1872) from the whole southern Africa, and possibly *C. ovamboana* Kaszab, 1981 from the border area between Namibia and Angola]. (b) The group of *C. angolensis* (Gemminger and Harold, 1870) is distributed from Kenya south to South Africa and west to Namibia, Angola and the Congo Basin. It includes at least: *C. angolensis* (with its synonym *Mylabris phalerata* Erichson, 1843, *nomen praeoccupatum*), *C. callicera* (Gerstaecker, 1870), *C. delagoensis* (Pic, 1909), *C. exclamationis* (Marseul,

1872) (and its possible synonym *Mylabris bivittata* Marseul, 1872), *C. matet-siensis* Kaszab, 1951, *C. pilosicollis* Borchmann, 1940, *C. pubicollis* Borchmann, 1940, *C. ruficrus* (Gerstaecker, 1854), *C. trifurca* (Gerstaecker, 1854), *C. tripunctata* Borchmann, 1940, and possibly *C. bilineata* (Marseul, 1879), *C. foveithorax* (Pic, 1912) and *C. ngamensis* (Pic, 1912).

Some other groups of species are endemic to some smaller Afrotropical areas. Endemic to the south-western Africa, primarily in xeric habitats of Namibia and South Africa are: (a) the group of *C. korana* Péringuey, 1888, which includes also *C. karroensis* Péringuey, 1909; (b-c) the apparently monotypic groups of *C. capensis* (Linnaeus, 1764) and of *C. groendali* (Billberg, 1813); (d) the group of *C. peringueyi* (Voigts, 1901), which includes also *C. braunsiana* Kaszab, 1958, *C. trifasciata* Pic, 1948, and possibly also *C. gariepina* (Péringuey, 1888) and *C. spuria* (Fähræus, 1870); (e) the group of *C. gyllenballi* (Billberg, 1813) which includes also *C. aliena* (Péringuey, 1892). Endemic to central Africa with an extension in southern Africa is the group of *C. interna* (Harold, 1870), which includes at least *C. angolana* Borchmann, 1940 (possible synonym of the following species), *C. blanda* (Péringuey, 1892), *C. basilewskyi* Kaszab, 1958, *C. congoana* (Duvivier, 1890). A few groups are distributed in southern central Africa (south Congo and Zambia) primarily.

The distribution of *Ceroctis* in our opinion is referable to a model explainable by the second biogeographical hypothesis previously discussed for the genus *Actenodia*. We hypothesize the origin of *Ceroctis* in Africa with a dispersal event to the Saharo-Mediterranean area along the eastern Africa savannah corridor during the late Pliocene, and a subsequent isolation of the northern Africa sub-range due to the extreme desertification of Sahara.

(c) The genus *Sitaris* Latreille, 1802

This genus belongs to a phyletic lineage of the tribe Nemognathini (see Bologna and Pinto, 2002), which in the previous literature (e.g. MacSwain, 1956; Kaszab, 1969; Bologna, 1991) was separated in a distinct tribe Sitarini with some other taxa of the Old World characterized by greatly modified adult morphology, but more primitive larval morphology and biology. All genera of the subfamily (possibly except the primitive tribe Stenoderini) have phoretic triungulins, which potentially permit a great dispersal capacity, but their complex larval biology and their strict relations with their bee host, actually tend to fragment their distribution, particularly in this Old World lineage (for a review see: Bologna, 1991; Bologna and Pinto, 2001).

The monophyly of *Sitaris* was doubted, but lacking molecular evidences, the morphology supports the maintenance of the genus. Two subgenera were described: the nominate and *Filalia* Martinez de la Escalera, 1906, monotypic sub-Saharan. According to unpublished data (Bologna and Di Giulio),

Sitaris includes about 16 Mediterranean species (one distributed also in central Europe), three from Central Asia (Iran, late Turkestan), six from Sahara and six from southern Africa. Moreover two isolated species, *S. bicoloritarsis* (Pic, 1939) and *S. bipartitus* (Pic, 1909), are endemic to Eritrea and Djibouti, another undescribed species was collected in southern Congo, and another, *S. atricornis* (Pic, 1922), is endemic to southern-east India.

The relationships among species are still not clarified and some appear to be very isolated in each area. For example: *S. (Filalia) cerambycinus* Martinez de la Escalera, 1906, discussed above; *S. (Sitaris) minutus* Pic, 1932 and a new species, respectively from western and southern Turkey, as concerns the Mediterranean area; *S. bushmanicus* Kaszab, 1953, in South Africa; *S. atricornis* in India.

Without a cladistic analysis we can not discuss the biogeography of this genus. As concerns the nominate subgenus, most Mediterranean species (Fig. 3) appear to form a group, phenetically distinct, even if constituted by different subgroups. Possibly, the Somalian, Eritrean and Congolese species, and two new species from Western Cape and Natal (South Africa), are related to the Mediterranean lineage. The Saharan species (Fig. 3) belong at least to two subgroups, one of which comprises a few small and very modified taxa. The morphology of one southern African species from the xeric habitat of Namaqualand (*S. bushmanicus*) greatly parallels that of these small Saharan species [*S. balachowskyi* (Pejerimhoff, 1931) and possibly *S. ferrantei*, Pic 1911], probably due to adaptive convergence. Interestingly the remaining South African species (*S. capensis* Péringuey, 1888, *S. fitsimonsi* Kaszab, 1951, *S. notaticollis* Péringuey, 1888) (Fig. 3) are very distinct or similar to the larger Saharan species.

The distribution of the genus *Sitaris* seems to be explainable according to the same model evidenced for the genus *Actenodia*, with a possible old (Miocenic or Pliocenic) separation of the primary range of the genus, due to the desertification of Sahara and distinct radiation, particularly in dry or mediterranean ecosystems of both Palaearctic and Afrotropical Regions.

(d) The genus *Stenoria* Mulsant, 1857

Stenoria belongs to the same lineage of *Sitaris* previously discussed. It represents a more derived taxon, particularly as concerns the larval morphology and biology. Triungulins are phoretic and larvae develop on bee nests, particularly of Colletidae, Andrenidae and Megachilidae. As in other Nemognathini of the sitarine lineage, adults have the apotypic condition of reduced elytra.

The genus includes two subgenera, the nominate and *Gineremia* Pardo Alcaide, 1961, with a single species [*S. (G.) saharica* Pardo Alcaide, 1961]. Close, or possibly synonym of this genus, is *Nyadatus* Aksentjev, 1981 from Central Asia.

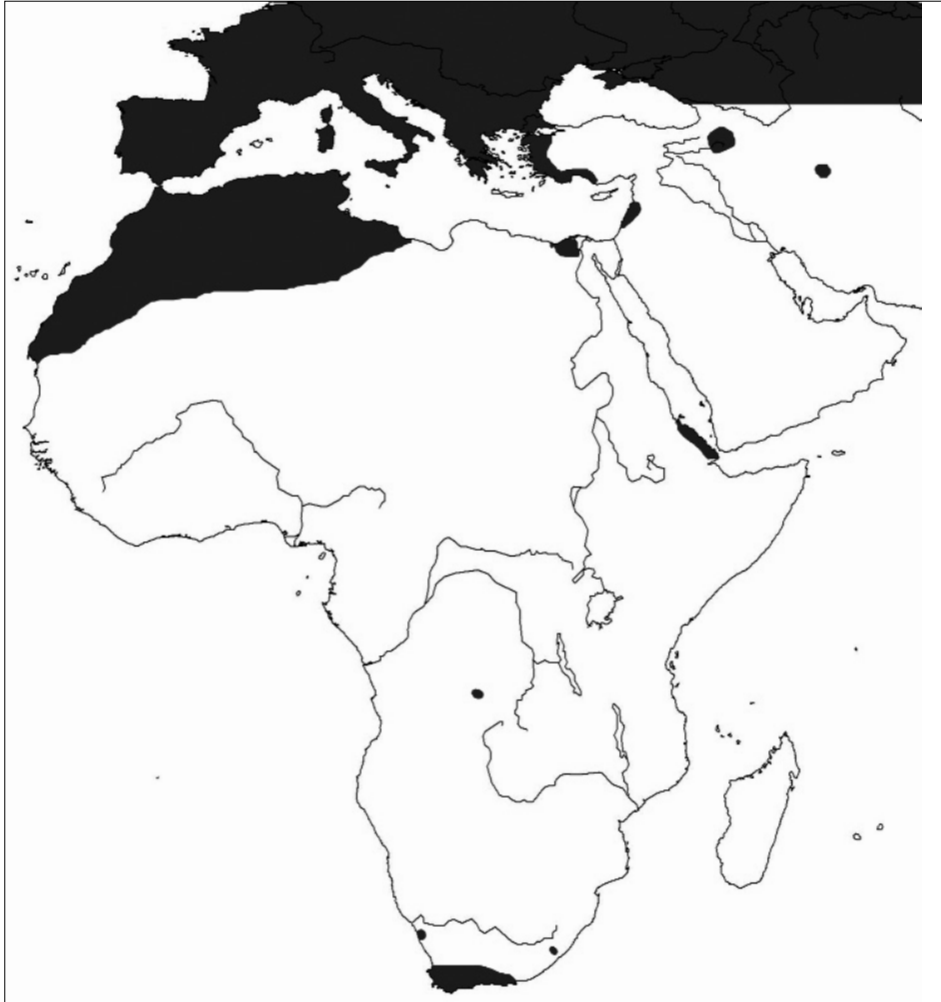


Fig. 3 - Distribution map of the genus *Sitaris*.

No revision of the genus were published and relationships of species are completely unknown, but according to the morphology, the monophyly of the genus seems to be supported. The distribution of *Stenoria* is similar to that of *Sitaris*, supporting the same biogeographical model. *Stenoria* includes 30 described taxa, some of doubtful value, distributed mostly in Central Asia, with nine species from Mediterranean and Saharan areas (Fig. 4), two of which, namely *S. analis* Schaum, 1859 and *S. apicalis* (Latreille, 1804), distributed also in central Europe. A few species are distributed in the Afrotropical region (Fig. 4): *S. muiri* Kaszab, 1956 in Yemen and possibly in Mozambique; *S. gib-*

bicollis Borchmann, 1940 in Kenya, Tanzania and South Africa; *S. hessei* Kaszab, 1953 in South Africa (Namaqualand), being another one from the same area (*S. discomaculata* Kaszab, 1953), probably referable to another genus (Bologna, unpubl.). This species from southern Africa is slightly distinct from both the Palaearctic and the East African species.

II. Taxa with disjunct ranges, primarily Mediterranean and with relict species in eastern Africa

As mentioned in the Introduction, a few taxa (genera, groups of species, species) of Meloidae have a primarily Mediterranean- Saharan distribution, with isolated species (or populations) in the eastern Africa. In our opinion, these isolated elements can be interpreted according to a single biogeographical model, being them relict of dispersal events, probably occurred during the Pleistocenic expansion of the xeric Mediterranean or the Saharan desert biomes, with a subsequent speciation (or fragmentation in the case of populations) due to the isolation produced by the intermediate expansion of savannah.

The dispersal of these lineages could have been occurred, for the Mediterranean elements, along the coasts of Egypt, south to Somalia, where relict of Mediterranean flora are possibly still present (Pichi-Sermolli, 1957). For the Saharan elements the dispersal could have been occurred along the coastal deserts of Sudan, Eritrea and Somalia. Another possibility, for the Saharo-Arabian elements, is the occurrence of Plio-Pleistocenic events of vicariance, due to the fragmentation of ancestral ranges, determined by the opening of the Strait of Aden. Some of these cases were partially discussed by Bologna (1990).

Among the subfamily Meloinae, the following examples concern the tribes Lyttini (a-b), Cerocomini (c), Epicautini (d), Mylabrini (e) and Meloini (f). One single case (g) concerns a genus of the subfamily Nemognathinae, tribe Nemognathini.

(a) The genus *Alosimus* Mulsant, 1857 is primarily Mediterranean with several species also in the Near East (to Iran and Afghanistan). Among the genus, *Alosimus somalicus* Kaszab, 1951 is endemic to Somalia (only the Holotype is known). It clearly belongs to the West Mediterranean group of *A. viridissimus* (Lucas, 1849), which includes three species from Maghreb, one from the coasts of central Italy (*A. tyrrhenicus* Bologna, 1989, possibly extinct) and the cited Somalian species (Bologna, 1989, 1990). Both these last two species have relict distribution out of Maghreb, probably due to the fragmentation of a late wider range of this group of species. Particularly, the presence of one species of the group in Somalia seems to be linkable to the described event of expansion of the mediterranean ecosystems during a pluvial Pleistocenic period.

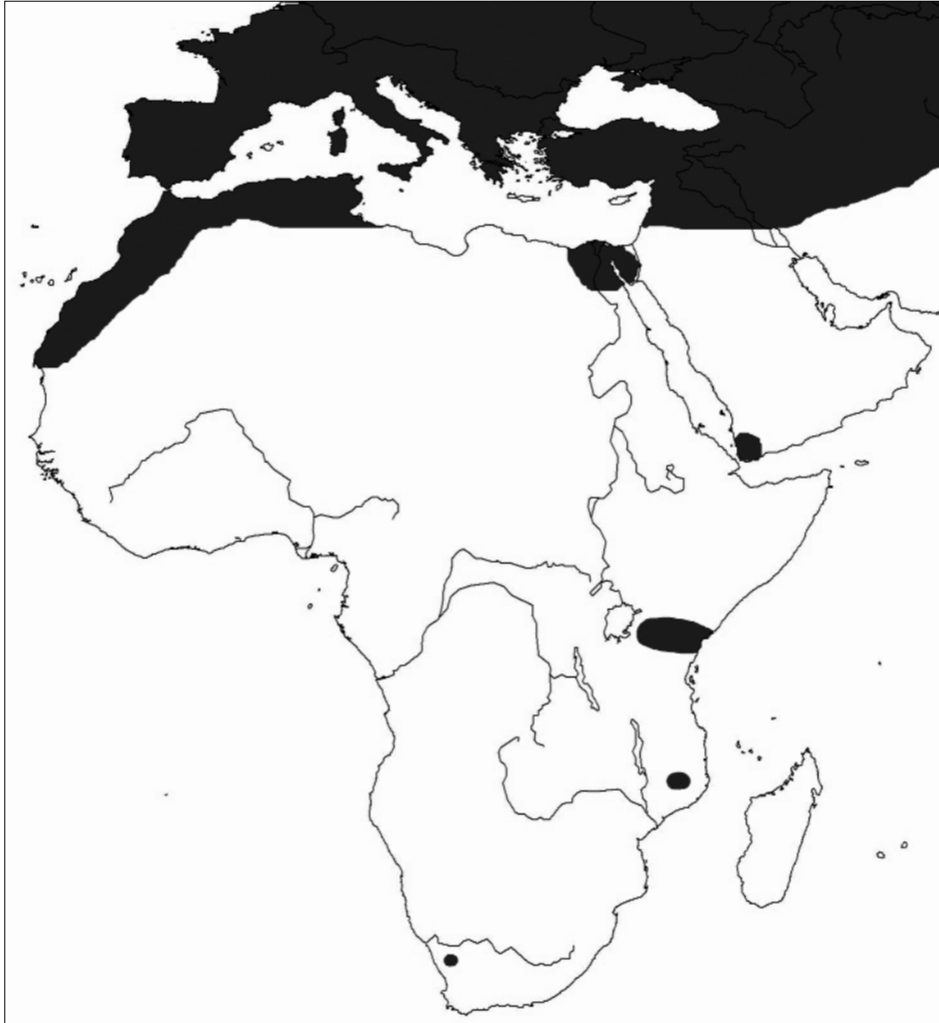


Fig. 4 - Distribution map of the genus *Stenoria*.

(b) The genus *Cabalia* Mulsant and Rey, 1858 (see Kaszab, 1983; Bologna, 1990; Bologna and Pinto, 2002) includes a few species: one from eastern Africa [*C. limbata* (Kolbe, 1894) originally described in the genus *Paroenas* Kolbe, 1894]; two from Ethiopia [*C. ruspolii* (Pic, 1914) erroneously cited from Somalia, with its possible synonym *C. aethiopica* Kaszab, 1981; *C. abyssinica* Kaszab, 1948]; one from Arabia (*C. arabica* Kaszab, 1983); one trans-Saharan [*C. rufiventris* (Walker, 1871), with its synonym *C. longicollis* Kaszab, 1948]; one western Saharan [*C. rubriventris* (Fairmaire, 1860)]; one from Maghreb and Sicily [*C. segetum* (Fabricius, 1792)].

The disjunct distribution of this genus (Fig. 5a) could be explained by the fragmentation of a late range due to desertification and subsequent events of vicariance and radiation in the isolated subranges. Alternatively, a dispersal event, along the Nile Valley or the Arabian Peninsula (in our opinion probably south to north) and subsequent radiations could be proposed.

(c) The complex of sister genera *Diaphorocera* Heyden, 1863 and *Somalarthrocera* Turco and Bologna, 2008, recently revised by Turco and Bologna (2007, 2008), represents another interesting example. They belong to the tribe Cerocomini, including 6 genera primarily Palaearctic. One genus is Turanian-Mediterranean (*Cerocoma* Geoffroy, 1762), one Turanian (*Rhampholyssa* Kraatz, 1863), three Saharo-Sindian (*Anisarthrocera* Semenow, 1895; *Diaphorocera*; *Rhampholyssodes* Kaszab, 1983). The genus *Somalarthrocera* includes one species from northern semi-desert Somalia [*S. semirufa* (Fairmaire, 1882), quoted as *Anisarthrocera* by Bologna, 1990], and one species from sub-coastal Kenya (*S. savanicola* Bologna and Turco, 2008). This genus represents the sister of *Diaphorocera*, distributed from Western Sahara to southern Iran, Palestine and Arabian Peninsula. Its presence in the Horn of Africa, could be related to a Pliocenic fragmentation of the ancestor range, due to a savannah pulsation, which produced a vicariance phenomenon of this possibly Palaearctic xeric lineage, after its spread in eastern Africa.

(d) *Epicauta sharpi* (Marseul, 1875) is a xeric species distributed in southern Iran, Jordan and south Israel and in the whole Arabian Peninsula, recorded also from Djibouti (Bologna, 1990). It belongs to a Saharo-Sindian group of species, including also *E. sanguiniceps* (Fairmaire, 1885) from Algeria and *E. textilis* (Haag-Rutenberg, 1880) from Iraq, Iran and Arabian Peninsula (Bologna and Turco, 2007). Its presence in the northern Somalia is probably referable to a Pleistocenic dispersal event from the Arabian Peninsula.

(e) *Croscherichia tigrinipennis* (Latreille, 1827) is a widespread species belonging to a Saharo-Sindian genus. It is widely distributed through the whole Sahara and in the Arabian Peninsula, with scarce penetration in the Sahel (Senegal, Sudan and few records from Ethiopia; Bologna and Coco, 1991). This example of distribution seems clearly referable to a recent dispersal event along the Nile Valley.

(f) Bologna (1990) described *Meloe (Eurymeloe) vignai* from Djibouti. This species belongs to a small group of Saharo-Arabian species of the subgenus *Eurymeloe* Reitter, 1911, which includes *M. (E.) saharensis* Chobaut, 1898, from the Algerian northern Sahara, its possible synonym *M. (E.) marianii* Kaszab, 1983 from northern Egypt and Saudi Arabia, and *M. (E.) otini* Peyerimhoff, 1949 from north-eastern Morocco. Also in this case the presence of this phyletic lineage in the northern xeric Somalia seems referable to a Pleistocenic dispersal event from the Arabian area.

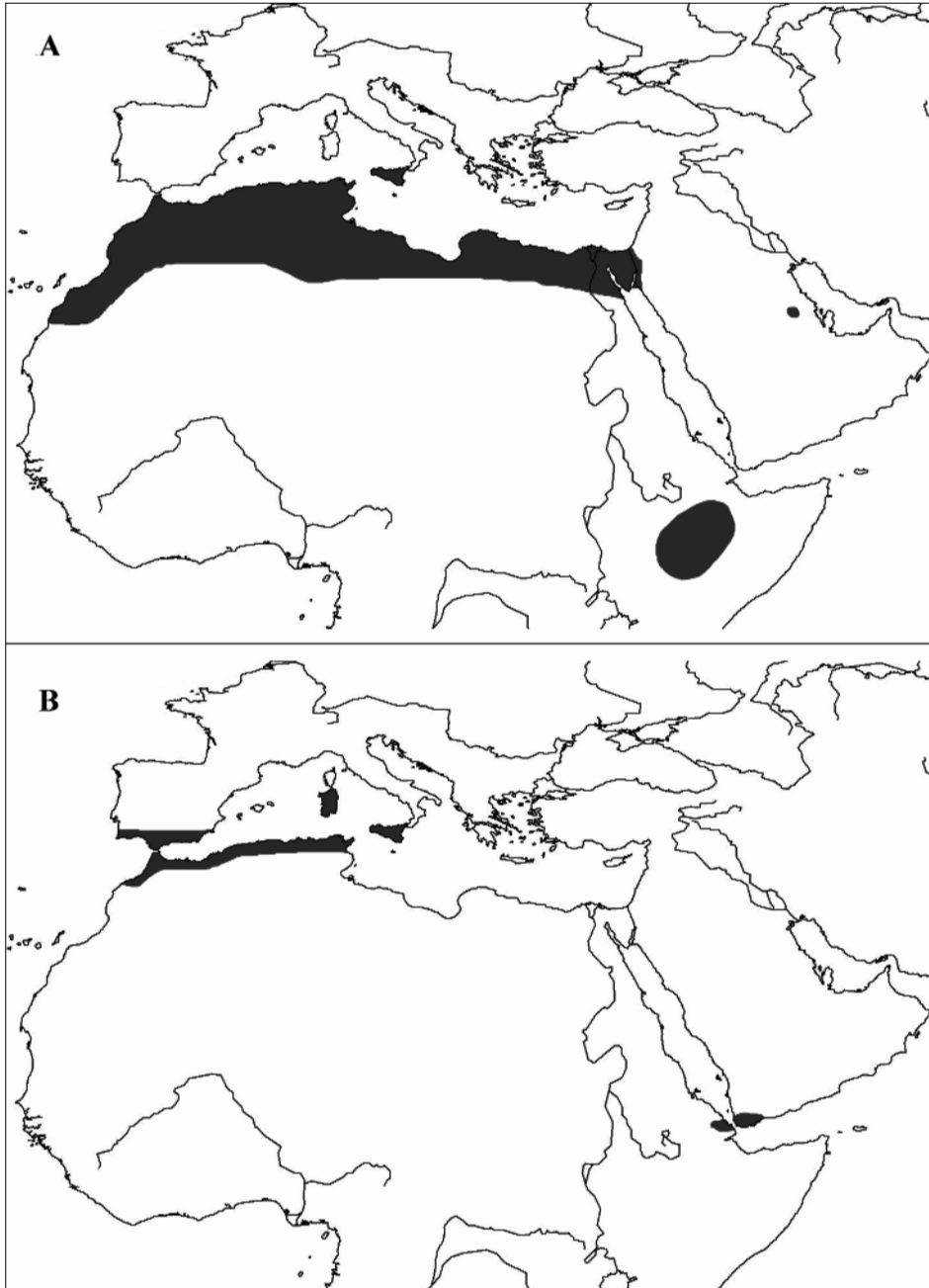


Fig. 5 - (a) Distribution map of the genus *Cabalia*. (b) Distribution map of the genus *Leptopalpus*.

(g) The genus *Leptopalpus* Guérin de Méneville, 1844 (see Bologna, 1991) includes only two species (Fig. 5b): *L. rostratus* (Fabricius, 1792) a western Mediterranean element (Iberian Peninsula, Maghreb, and possibly extinct, in Sardinia and Sicily); and *L. quadrimaculatus* Gahan, 1896, from Yemen and Eritrea (Bologna, 1990). The distribution of *Leptopalpus* seems a relict condition of a previous wider range clearly fragmented by the Pleistocene extension of the Sahara desert. The actual relationships of this genus are completely unclear, but usually it is referred to a Palearctic lineage. In this case, its presence on both shores of the Bab al Mandab, of one species of this genus clearly supports the hypothesis of a recent dispersal event from the Arabian Peninsula.

CONCLUSIONS

The survey of examples we discussed above permits some biogeographical considerations on the hypothesized “Mediterranean-southern African disjunct model” (see Introduction of the volume: Bologna et al., 2008c).

The first remark is that it does not exist among Meloidae a distributional disjunct model with only Mediterranean and South African related species, as known in other groups of animals and plants. On the contrary we detected some cases of genera, which have the greatest diversity in these two areas, but also a few species in eastern Africa (*Actenodia*, *Sitaris*, *Stenoria*), even if isolated and with narrow ranges. Another genus (*Ceroctis*) is largely distributed also in central Africa and has only one species north to Sahara, and two in the Arabian Peninsula. In none of these cases are present species in Western Africa or in the Sahel and all taxa seem typically distributed in open habitats. In the Afrotropical countries the species inhabit a variety of ecosystems, such as mediterranean maquis, savannahs, semideserts, while in the Palearctic countries they colonize desert and other xeric ecosystems, or mediterranean type vegetation.

The second remark is that this type of disjunct distribution seems referable to convergent biogeographical phenomena more than a single vicariance event, which separated a late biota. In our opinion we can consider an African origin for both Mylabrini genera, the ranges of which have been isolated by distinct events of desertification of the Sahara region, probably Miocenic in the case of *Actenodia*, and Pliocenic in that of *Ceroctis*. According to a dispersal interpretation, both genera had an Afrotropical origin and distinct late dispersal to northern African lands along an eastern African corridor, followed by the fragmentation of their range due to the desertification. Both the Nemognathini examples seem to highlight similar, distinct, vicariance events, probably after dispersal from Mediterranean along the eastern Africa. The reduced presence in northern east Africa (few species all with narrow ranges) of both the contingents of genera (Afrotropical and Palearctic) is probably

due to repeated phenomena of pulsations of the forest ecosystems in this zone during hot periods, which shared out the populations and produced speciations and extinctions, except in the driest and peripheral areas.

Another evaluation concerns the second type of distribution model we presented in this work: a northern Palaearctic origin of some genera, possibly except for the complex *Diaphorocera-Somalathrocera*, being the origin of the tribe Cerocomini doubtful and, according to molecular evidences (Bologna et al., 2008b), possibly Afrotropical. Also in the case of the genus *Cabalia* an Afrotropical vs a Palaearctic origin could be hypothesized. This model of distribution, even if different from the previous one, would support the hypothesis of the existence of an eastern African corridor used by some taxa for dispersal events. This corridor therefore was active not only during a late Tertiary period (Miocene-first Pliocene), but also more recently (late Pliocene-Pleistocene).

Among the examples concerning the second type of distribution, the presence of endemic species also in the xeric Somalia (*Alosimus somaliensis*, *Meloe vignai*) seems referable to older dispersal events, while the presence of isolated populations on both shores of the Aden Strait (*Epicauta sharpi*, *Leptopalpus quadrimaculatus*) or in Ethiopia - as apical point of expansion along the Nile Valley (*Croscherichia tigrinipennis*) - represents the evidence of Pleistocenic dispersal during glacial periods.

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