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# Mediterranean-southern African disjunct distribution and flea beetles: the example of the “black species” of *Longitarsus* associated with Boraginaceae (Coleoptera, Chrysomelidae, Alticinae)

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Key words. Alticinae, Boraginaceae, Afrotropical Region, *Longitarsus*, Mediterranean area, disjunct distribution.

## SUMMARY

In this paper the disjunct distribution of two *Longitarsus* species-groups associated with Boraginaceae: *capensis*-group, restricted to the southern Africa and presently including 15 species, and *anchusae*-group (sensu Biondi, 1995), widespread in the western Palaearctic area with 4 species, is discussed. Some hypotheses explaining the separate distributions of Mediterranean and South African groups are proposed. Finally, the host-plant shift from native *Lobostemon* spp. to the introduced plant *Echium plantagineum* L. shown by some species of the *capensis* group is also discussed.

## INTRODUCTION

*Longitarsus* Latreille, as described in Berthold (1827), is presently the largest genus within Chrysomelidae, Alticinae with about 600 known species occurring throughout all zoogeographical regions (Biondi & D’Alessandro, 2008).

This flea beetle genus is well represented in the Mediterranean area (about 160 species), where is better known from an autecological standpoint (Biondi, 1996). *Longitarsus* species occurring in the Mediterranean area are known to feed, as adults, on plants of different botanical families, the preferred being Boraginaceae (26.4%), Lamiaceae (24.9%), Asteraceae (13.8%), Plantaginaceae (9.5%), and Scrophulariaceae (9.5%) (Fig. 1). Particularly, species-groups, such as *aeneus*, *anchusae*, *exsoletus* and *echii* feeding on Boraginaceae, show an elevated degree of trophic specialization (Jolivet & Hawkeswood, 1995; Biondi, 1996) and include mainly oligotopic species, generally termophilous (Figs 2-3). In the

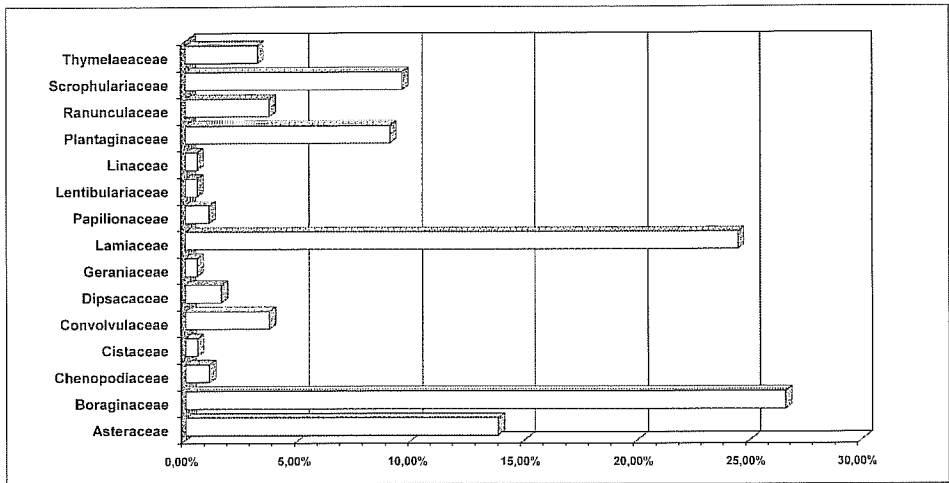


Fig. 1 - Percentages of the Mediterranean *Longitarsus* species for host botanical families in the Mediterranean area (redraw from Biondi, 1996).

Mediterranean area, in fact, 34% of the *Longitarsus* species associated with Boraginaceae are monophagous (feed on one or two closely related botanical genera), 56% oligophagous (feed on more botanical genera of one or two closely related families) and only 10% polyphagous (feed on many botanical species not closely related). The trophic categories are those proposed by Biondi (1996) and Fernandez & Hilker (2007). Therefore, in the Mediterranean area 90% of the *Longitarsus* species associated with Boraginaceae (34% monophagous and 56% oligophagous) feed exclusively on them (Biondi, 1996) (Fig. 3). In the Afrotropical Region, the genus *Longitarsus* presently includes about 120 described species, but many other yet undescribed taxa exist (Biondi, unpubl. data). Auto-ecological data available for the Afrotropical species of this flea beetle genus are extremely scarce or completely lacking if compared to the Mediterranean species. In the literature there are only a few reports of *Longitarsus* species associated with Boraginaceae in the sub-Saharan Africa, namely *Longitarsus punctifrons* Weise, 1895 (= *gossypii* Bryant, 1941) collected on *Heliotropium* sp. (Furth, 1985), and species of the *capensis* group collected on *Lobostemon* spp., *Anchusa capensis* Thumb., *Echium plantagineum* L. and *Heliotropium* sp. (Biondi, 1999; Biondi & D'Alessandro, 2008).

This paper includes some observations about the distribution of two *Longitarsus* species-groups associated with Boraginaceae: *capensis*-group, restricted to the southern Africa and presently including 15 species, and *anchusae*-group (sensu Biondi, 1995), widespread in the western Palaearctic area with 4 species (see list below) (Fig. 6).

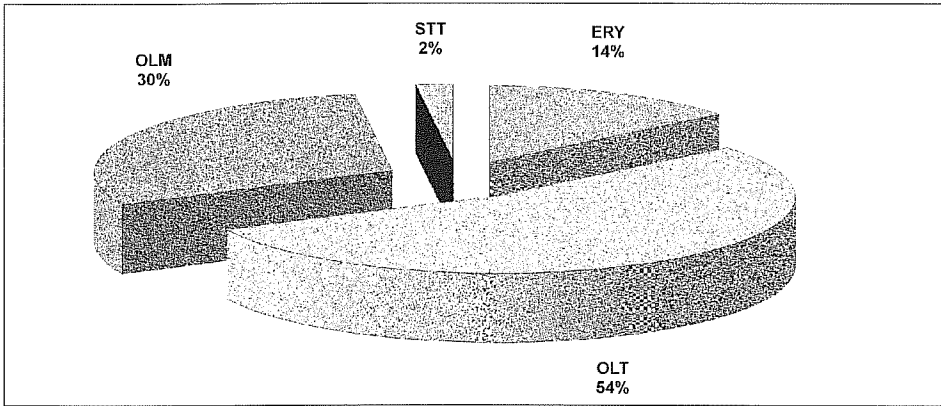


Fig. 2 - Percentages of ecological categories, based on environmental preferences, in the Mediterranean *Longitarsus* species associated with Boraginaceae. ERY: eurytopic; OLM: oligotopic-mesophilous; OLT: oligotopic-termophilous; STT: stenotopic-thermophilous.

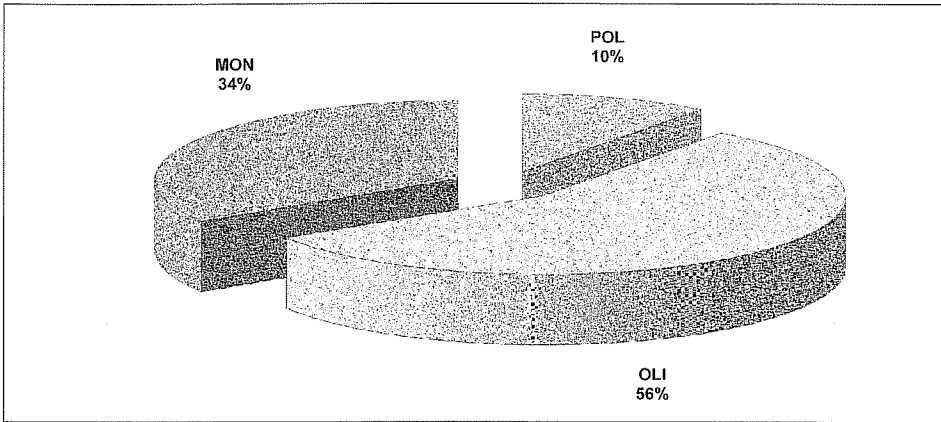


Fig. 3 - Percentages of trophic categories in the Mediterranean *Longitarsus* species associated with Boraginaceae. POL: polyphagous; OLI: oligophagous; MON: monophagous.

The most part of zoogeographical and autecological data on the species of the *Longitarsus capensis*-group reported in this contribution were collected during zoological collecting trips that were part of an Italian research project (PRIN 2004057217) aimed at interpreting the disjunct distribution of different plant and animal groups in the Mediterranean-South African regions (cf. Balinsky, 1962; La Greca, 1970, 1990; Axerold & Raven, 1978; Jürgens, 1997; Coleman et al., 2003).

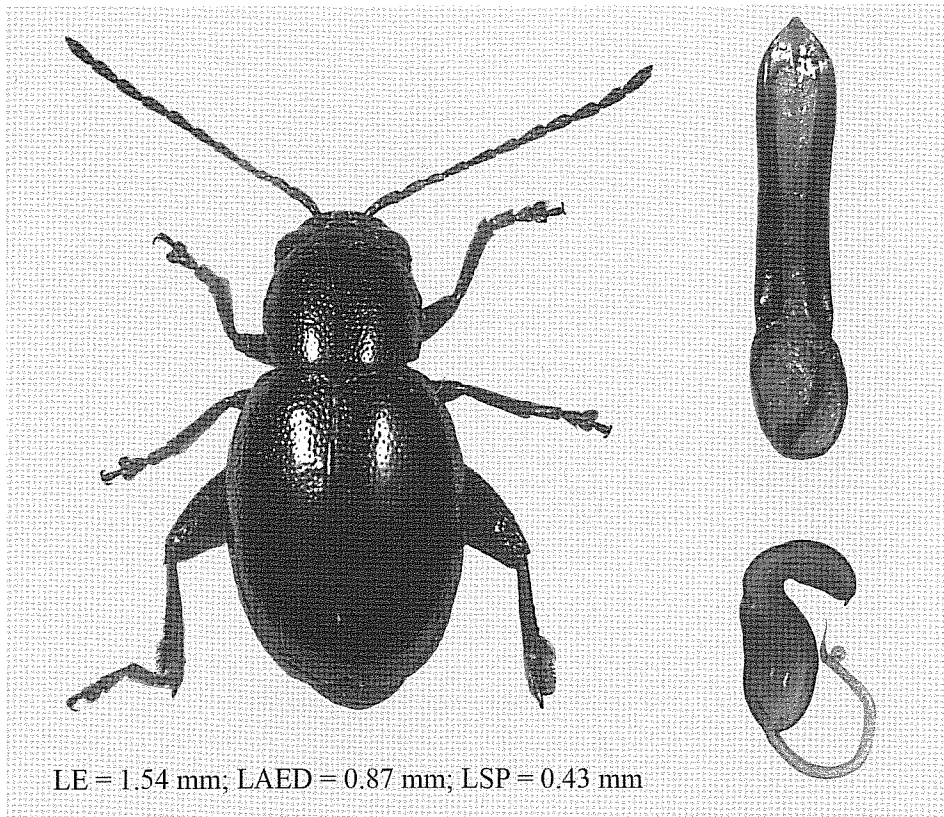


Fig. 4 - Habitus, median lobe of aedeagus, and spermatheca of *Longitarsus afromeridionalis* Biondi & D'Alessandro, 2008, a member of the South African *capensis* species-group. LE: length of the elytra; LAED: length of the median lobe of aedeagus; LSP: length of the spermatheca.

#### COMMENTED LIST OF THE SPECIES

##### **capensis species-group:**

##### *Longitarsus afromeridionalis* Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the southern-western coastal area of the Western Cape Province (Republic of South Africa) (Fig. 7).

**Host plants.** Boraginaceae: *Lobostemon* cf. *lucidus* (Lehm.) H. Bueck.

**Trophic range.** Monophagous.

**Phenology.** September (Tab. I).

##### *Longitarsus capensis* Baly, 1877

*Longitarsus capensis*: Biondi, 1999; Biondi & D'Alessandro, 2008

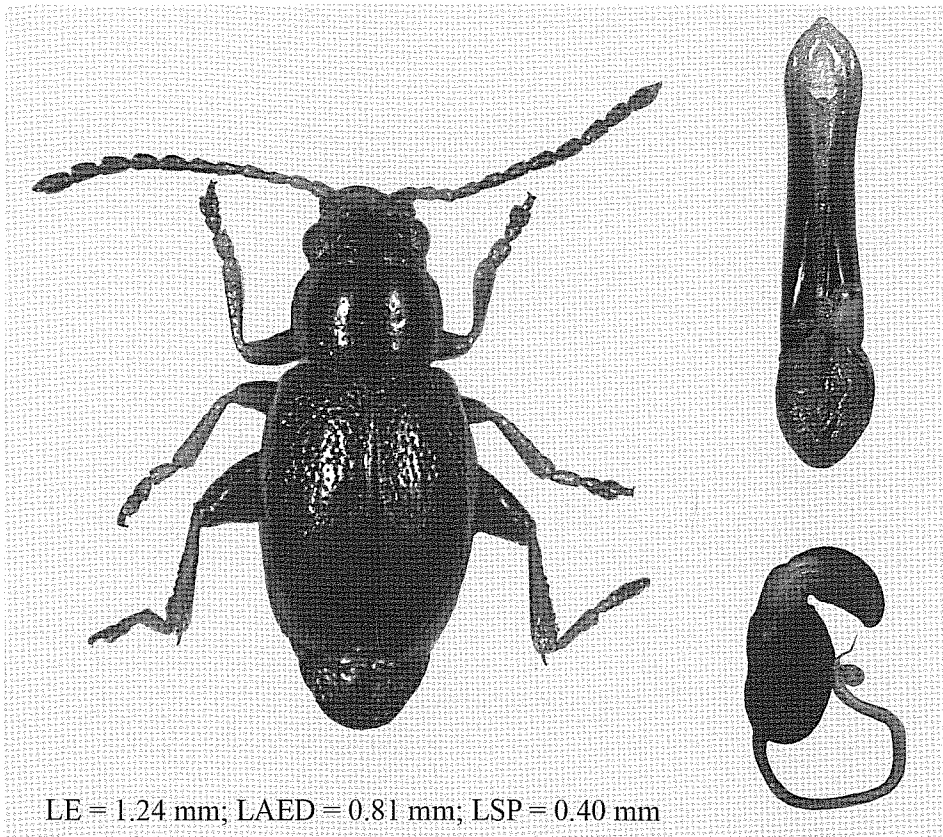


Fig. 5 - Habitus, median lobe of aedeagus, and spermatheca of *Longitarsus anchusae* (Paykull, 1799), a member of the West Palaearctic *anchusae* species-group. LE: length of the elytra; LAED: length of the median lobe of aedeagus; LSP: length of the spermatheca.

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the western part of the Western Cape Province (Republic of South Africa) (Fig. 7).

**Host plants.** Boraginaceae: *Lobostemon fruticosus* (L.) H. Buek, *L. cf. lucidus*, *Anchusa capensis* Thumb. and *Echium plantagineum* L.

**Trophic range.** Oligophagous.

**Phenology.** July, September, October (Tab. I).

***Longitarsus cedarbergensis* Biondi, 1999**

*Longitarsus cedarbergensis*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Cedarberg area (Republic of South Africa: Western Cape Province) (Fig. 7).

Host plants. Boraginaceae: *Lobostemon* cf. *dorotheae* M. H. Buys.  
Trophic range. Monophagous.  
Phenology. September (Tab. I).

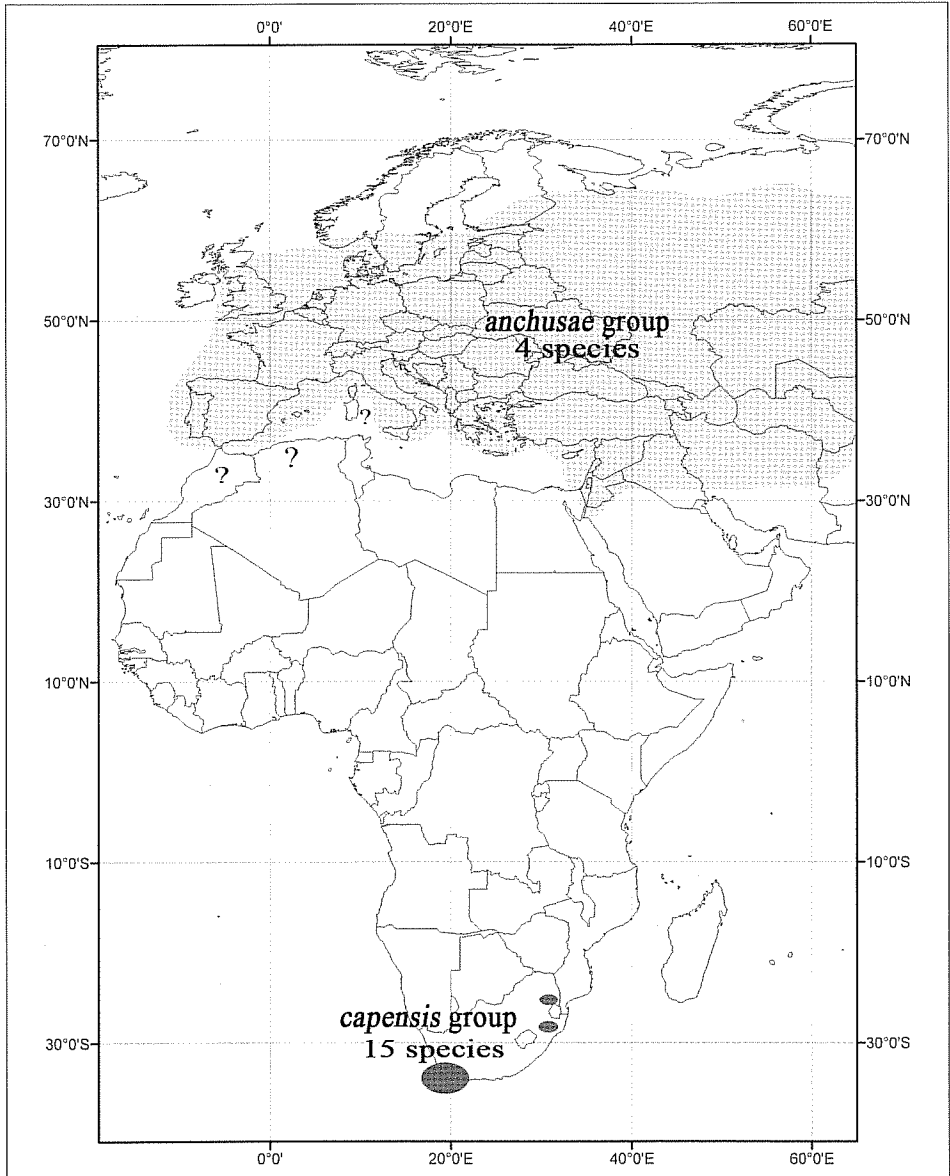


Fig. 6 - General distribution of the *Longitarus* species of the South African *capensis* group and the West Palearctic *anchusae* group.

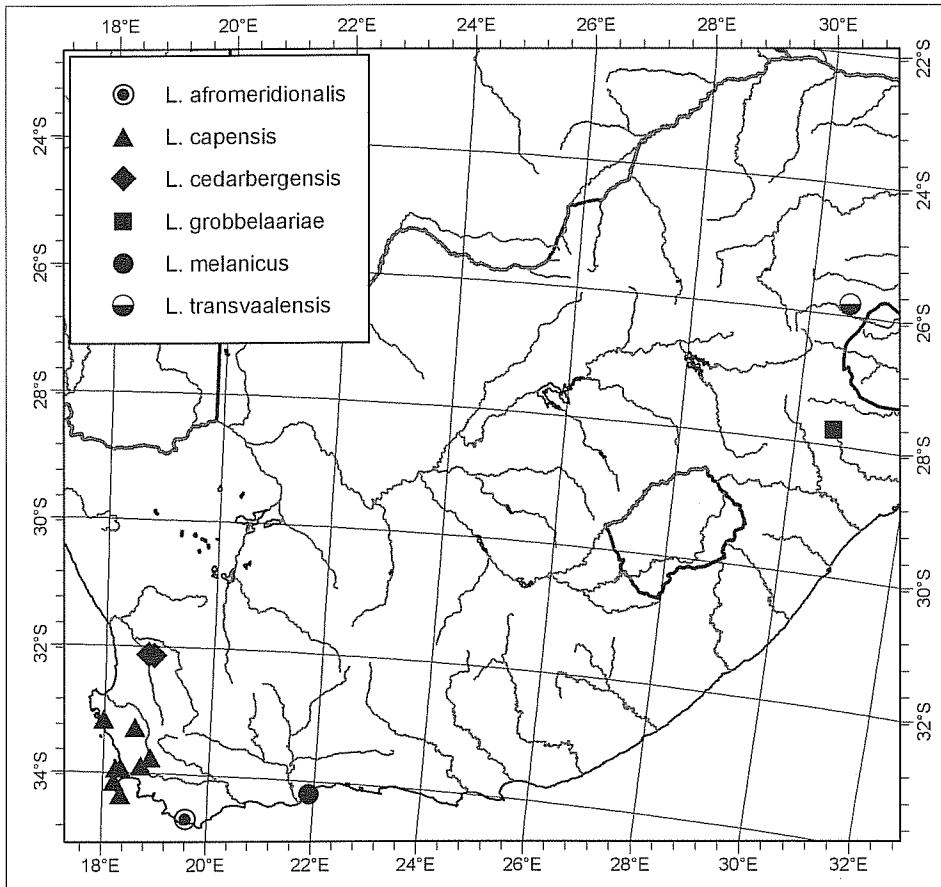


Fig. 7 - Distribution of: *Longitarsus afrimeridionalis* Biondi & D'Alessandro, *L. capensis* Baly, *L. cedarbergensis* Biondi, *L. grobbelaariae* Biondi & D'Alessandro, *L. melanicus* Biondi and *L. transvaalensis* Biondi.

***Longitarsus debiasei* Biondi & D'Alessandro, 2008**

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Langeberg area (Republic of South Africa: Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Echium plantagineum*.

**Trophic range.** Monophagous (?).

**Phenology.** October (Tab. I).

***Longitarsus grobbelaariae* Biondi & D'Alessandro, 2008**

**Distribution.** Southern-Eastern Afrotropical element (cf. Biondi & D'Alessandro, 2006) distributed in Kwazulu-Natal (Republic of South Africa) (Fig. 7).



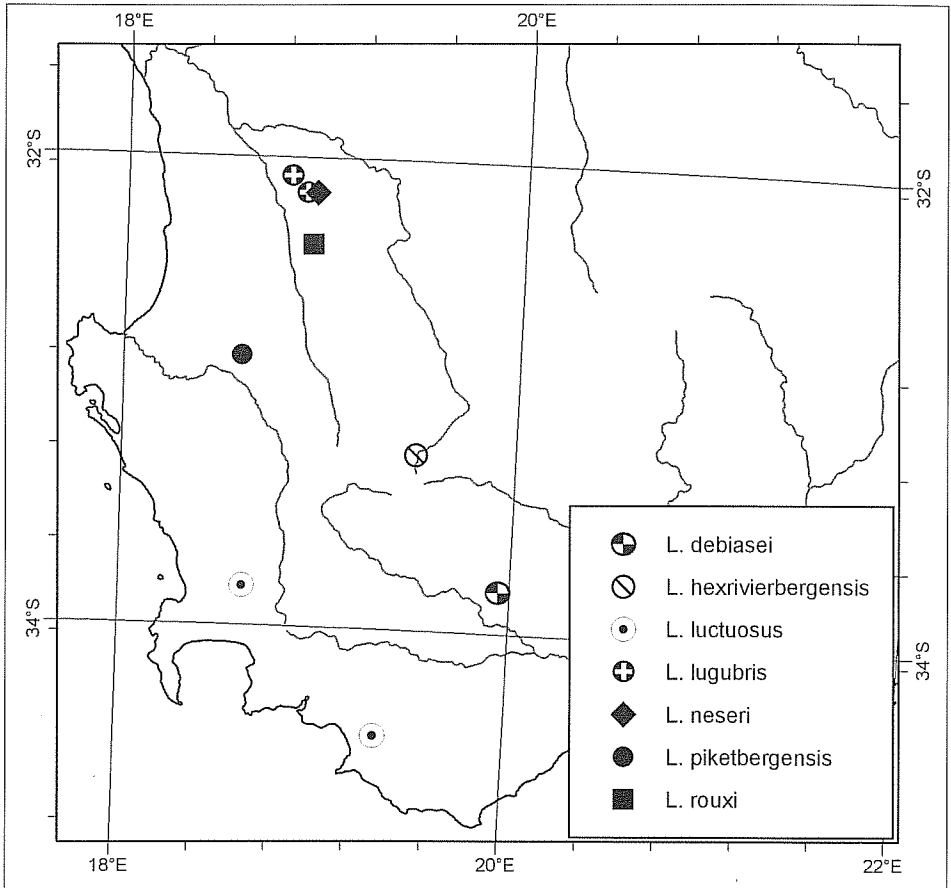


Fig. 8 - Distribution of: *Longitarsus debiasei* Biondi & D'Alessandro, *L. hexrivierbergensis* Biondi & D'Alessandro, *L. luctuosus* Biondi, *L. lugubris* Biondi, *L. neseri* Biondi, *L. piketbergensis* Biondi & D'Alessandro and *L. rouxi* Biondi & D'Alessandro.

**Host plants.** Boraginaceae: *Heliotropium* sp.

**Trophic range.** Monophagous.

**Phenology.** January, February (Tab. I).

***Longitarsus hexrivierbergensis* Biondi & D'Alessandro, 2008**

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Hexrivierberg area (Republic of South Africa: Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Echium plantagineum*.

**Trophic range.** Monophagous (?).

**Phenology.** October (Tab. I).

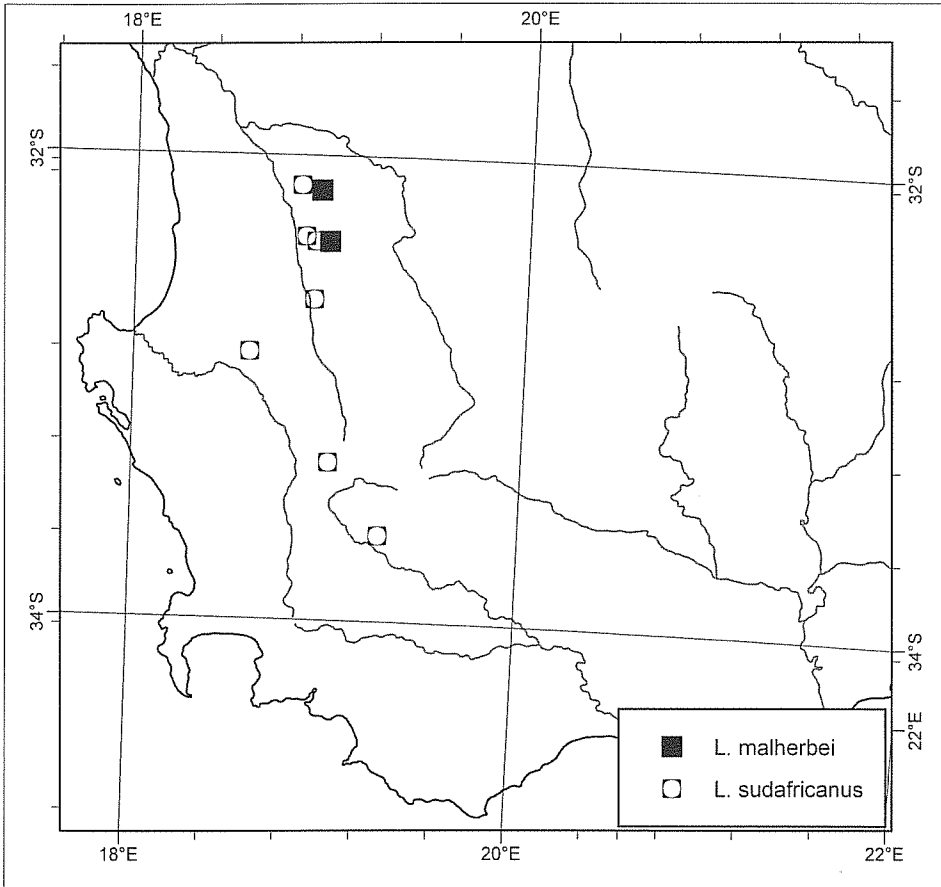


Fig. 9. Distribution of: *Longitarsus malherbei* Biondi & D'Alessandro and *L. sudafricanus* Biondi & D'Alessandro.

***Longitarsus luctuosus* Biondi, 1999**

*Longitarsus luctuosus*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the southern-western part of the Western Cape Province (Republic of South Africa) (Fig. 8).

**Host plants.** Boraginaceae: *Echium plantagineum*.

**Trophic range.** Monophagous (?).

**Phenology.** July, September (Tab. I).

***Longitarsus lugubris* Biondi, 1999**

*Longitarsus lugubris*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi &

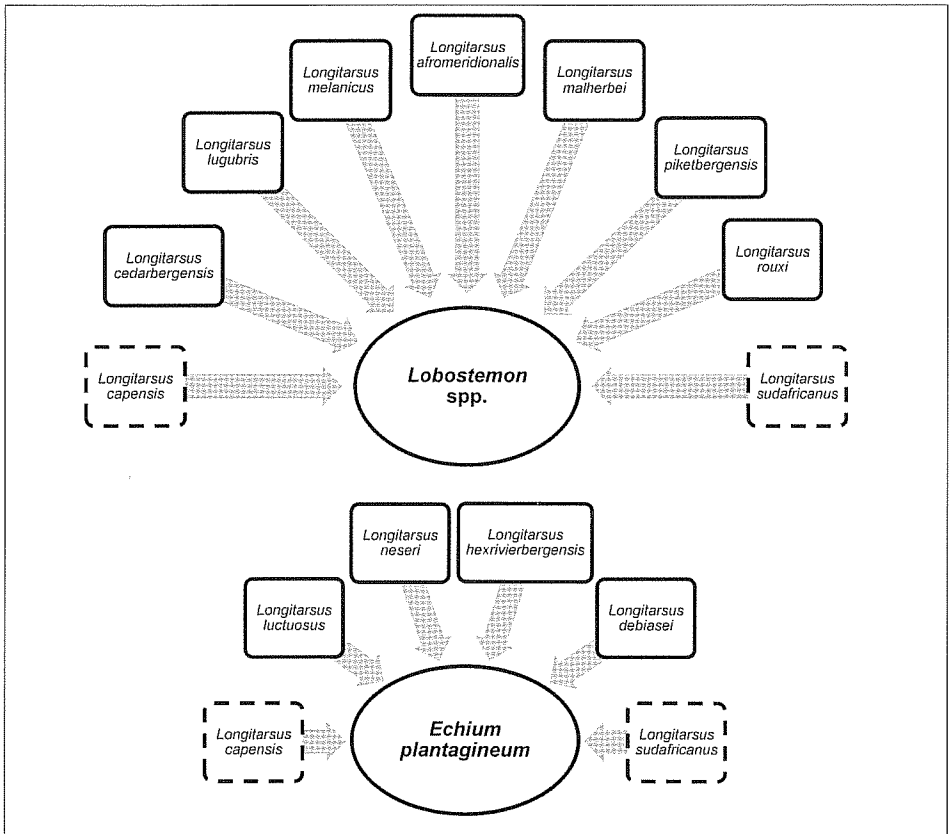


Fig. 10. Host-plants of the South African *Longitarsus capensis* species-group.

D'Alessandro, 2006), distributed in the Bokkeveldeberg and Cedarberg areas (Republic of South Africa: Northern and Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Lobostemon* cf. *dorotheae* and *L.* cf. *trichotomus* (Thumb.) DC.

**Trophic range.** Monophagous.

**Phenology.** September (Tab. I).

#### *Longitarsus malherbei* Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Cedarberg area (Republic of South Africa: Western Cape Province) (Fig. 9).

**Host plants.** Boraginaceae: *Lobostemon* cf. *dorotheae* and *L.* cf. *trichotomus*.

**Trophic range.** Monophagous.

**Phenology.** September (Tab. I).

Tab. 1 - Phenology of the *Longitarsus* species of the South African *capensis* group and the West Palearctic *anchusae* group. Light grey rectangles indicate negative samplings in places where the species was previously collected.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AGO	SEP	OCT	NOV	DEC
<i>capensis</i> species-group												
<i>afromeridionalis</i>									█	█		
<i>capensis</i>							█		█	█		
<i>cedarbergensis</i>									█			
<i>debiasei</i>									█	█		
<i>grobbellaariae</i>	█	█										
<i>hexrivierbergensis</i>									█	█		
<i>luctuosus</i>							█		█	█		
<i>lugubris</i>									█	█		
<i>malberbei</i>									█	█		
<i>melanicus</i>									█	█		
<i>neseri</i>							█			█		
<i>piketbergensis</i>									█	█		
<i>rouxi</i>				█					█	█		
<i>sudafricanus</i>									█	█		
<i>transvaalensis</i>		█										█
<i>anchusae</i> species-group												
<i>anatolicus</i>					█	█	█					
<i>anchusae</i>			█	█	█	█	█	█				
<i>hittita</i>					█	█	█					
<i>saulicus</i>		█	█	█	█							

***Longitarsus melanicus* Biondi, 1999**

*Longitarsus melanicus*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the southern coastal area of the Western Cape Province (Republic of South Africa) (Fig. 7).

**Host plants.** Boraginaceae: *Lobostemon* cf. *marlothii* Levyns.

**Trophic range.** Monophagous.

**Phenology.** September (Tab. I).

*Longitarsus neseri* Biondi, 1999

*Longitarsus neseri*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Piketberg area (Republic of South Africa: Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Echium plantagineum*.

**Trophic range.** Monophagous (?).

**Phenology.** July (Tab. I).

*Longitarsus piketbergensis* Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Piketberg area (Republic of South Africa: Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Lobostemon fruticosus*.

**Trophic range.** Monophagous.

**Phenology.** September (Tab. I).

*Longitarsus rouxi* Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the Cedarberg area (Republic of South Africa: Western Cape Province) (Fig. 8).

**Host plants.** Boraginaceae: *Lobostemon* sp., probably *L.* cf. *dorotheae* or *L.* cf. *trichotomus*.

**Trophic range.** Monophagous.

**Phenology.** April, September (Tab. I).

*Longitarsus sudafricanus* Biondi & D'Alessandro, 2008

**Distribution.** Southern-Western Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in the western mountain areas of the Western Cape Province (Republic of South Africa) (Fig. 9).

**Host plants.** Boraginaceae: *Lobostemon* cf. *dorotheae*, *L. fruticosus*, *L.* cf. *trichotomus* and *Echium plantagineum*.

**Trophic range.** Oligophagous.

**Phenology.** September (Tab. I).

***Longitarsus transvaalensis* Biondi, 1999**

*Longitarsus transvaalensis*: Biondi & D'Alessandro, 2008

**Distribution.** Southern-Eastern Afrotropical element (cf. Biondi & D'Alessandro, 2006), distributed in Mpumalanga Province (Republic of South Africa) (Fig. 7).

**Host plants.** This species was collected at forest edge on leaves of an unidentified plant belonging to the Borage family.

**Trophic range.** Monophagous (?).

**Phenology.** December (Tab. I).

***anchusae* species-group:**

***Longitarsus anatolicus* Weise, 1900**

*Longitarsus anatolicus*: Biondi, 1995, 1996; Gruev & Döberl, 1997, 2005.

**Distribution.** Central Asiatic element (cf. Vigna Taglianti et al., 1999), extended to the Anatolian region and Bulgaria.

**Host plants.** Boraginaceae: *Anchusa* spp.

**Trophic range.** Monophagous.

**Phenology.** May, June (Tab. I).

***Longitarsus anchusae* (Paykull, 1799)**

*Longitarsus anchusae*: Biondi, 1995, 1996; Gruev & Döberl, 1997, 2005.

**Distribution.** European element (Vigna Taglianti et al., 1999), extended to western Asia.

**Host plants.** Boraginaceae: *Anchusa* spp., *Asperugo* sp., *Buglossoides arvense* (L.) Johnst., *Cerinth* sp., *Cynoglossum* spp., *Echium plantagineum*, *Myosotis* sp., *Nonnea* sp., *Pulmonaria* sp., *Solenanthus* (?) sp., *Symphytum* spp.

**Trophic range.** Oligophagous.

**Phenology.** March, April, May, June, July (Tab. I).

***Longitarsus hittita* Biondi, 1995**

*Longitarsus hittita*: Biondi, 1996; Gruev & Döberl, 1997, 2005.

**Distribution.** Anatolian endemic element (cf. Vigna Taglianti et al., 1999), known from Turkey.

**Host plants.** Boraginaceae: *Solenanthus stamineus* (Desf.) Wettst.

**Trophic range.** Monophagous.

**Phenology.** May, June (Tab. I).

***Longitarsus saulicus* Gruev & Döberl, 2005**

= *Longitarsus morio* Sahlberg, 1913: Biondi, 1995, 1996; Gruev & Döberl, 1997.

**Distribution.** E-Mediterranean element (cf. Vigna Taglianti et al., 1999), distributed in Israel and Jordan.

**Host plants.** Boraginaceae: *Alkanna strigosa* Boiss. & Hohen., *Anchusa* spp., *Cynoglossum creticum* Miller, *Echium glomeratum* Poiret, *Symphytum palestinum* Boiss.

**Trophic range.** Oligophagous.

**Phenology.** February, March, April (Tab. I).

## DISCUSSION

Both these *Longitarsus* species-groups here considered, containing exclusively species with a black integument, are strictly associated with Boraginaceae generally in thermophilous environments, and share the following updated morphological characteristics that differentiate the *anchusae* and *capensis* groups within *Longitarsus* (Biondi, 1999; Biondi & D'Alessandro, 2008): i) head with impunctate vertex and frons with some large punctures impressed near the frontal grooves; ii) elytra apically subtruncate or widely and independently rounded; iii) humeral callus always completely absent in *capensis*-group, rarely developed in *anchusae*-group; iv) hind wings strongly reduced (species always subapterous in *capensis*-group; brachypterous, sub-brachypterous or very rarely macropterous in *anchusae*-group); v) large spermatheca (generally longer than 0.30 mm) with ducts often widely arcuate and usually uncoiled or with one coil, very rarely with two coils; vi) median lobe of aedeagus strongly sclerotized, mostly with a distinct apical median small tooth and a ventral sulcus invariably with clear impressions; vii) impressed elytral punctation generally dense and without signs of striae even in sutural area. The latter character is very important for distinguishing the species of the *anchusae* and *capensis* groups from the black species of *Longitarsus* associated with Lamiaceae, common in both the Mediterranean area and southern Africa.

Species of the *capensis* and *anchusae* groups are remarkably similar (Figs 4-5). In fact there is only one morphological trait, namely the degree of metathoracic wing reduction, that distinguishes the two groups; only subapterous species are known in the *capensis* species-group whereas brachypterous, sub-brachypterous or macropterous species can be found in the *anchusae* species-group. The similarities, if shown to be synapomorphic by a future phylogenetic analysis, might suggest that the two groups comprise a monophyletic unit whose Mediterranean and South African subgroups became geographically separated relatively recently.

Alternative hypotheses could explain the separate distributions of Mediterranean and South African *anchusae* and *capensis* species-groups. This particular type of distribution is widely documented for many plant and ani-

mal groups (cf. Balinsky, 1962; La Greca, 1970, 1990; Axerold & Raven, 1978; Jürgens, 1997; Coleman et al., 2003). Excluding unlikely recent long-distance dispersal events, the most probable hypothesis to explain this type of geographical distribution is to accept there were ecological connections between the Mediterranean and South African areas in the past. Species in the *capensis*-group are significantly associated with “fynbos”, a Mediterranean-type of vegetation that is widespread in the south-western part of South Africa and probably formed no earlier than the Late Miocene (cf. Axelrod & Raven, 1978; Richardson et al., 2001). Based on this observation, the migratory flow of one or more Mediterranean *capensis* ancestors from the north towards South Africa may have occurred during the Quaternary period via “arid corridors” (sensu Balinski, 1962) which “appeared” in eastern Africa due to climatic changes that took place in the Northern Hemisphere during the glacial periods (cf. Jürgens, 1997).

In the Cape region, the *capensis* species-group radiated into different species, often confined to rather limited areas (Figs 7-9). In the Mediterranean, during the Quaternary period, species diversification was very limited in the *anchusae*-group, as well as in other closely related species-groups (cf. Biondi, 1995). This occurrence is frequent in many plant and animal groups in the Cape region, which have a comparatively high biodiversities compared with ecologically similar areas. Different factors have been suggested to explain this phenomenon: (1) topographical complexity; (2) edaphic complexity; (3) pollinator specialization; (4) fire; and (5) short dispersal distance (Barraclough, 2006).

Mediterranean-type ecosystems are included among the main biodiversity hot spots around the world (Myers et al., 2000; Goldblatt & Manning, 2002) and fire is considered one of the main drivers of diversification in these ecosystems. Recurrent fires over millions of years, with an average frequency of about 15-50 per year, have been suggested to trigger dramatic diversification by selecting taxa with short generation times and/or to instigate the isolation of populations (Verdù et al., 2007). In our opinion, the high number of species in the *capensis*-group in such a restricted geographic area can be explained by the important role fire played in leading to the evolution of different life history strategies and driving the process of speciation or local extinction in fynbos plants and in animals associated with them.

As mentioned above, species of the *capensis*-group are primarily associated with fynbos and plants of the genus *Lobostemon* (Boraginaceae). *Lobostemon* includes perennial shrubs with alternating leaves and flowers, mostly bell-shaped and usually pink or blue. This genus includes twenty-eight species endemic to South Africa and is largely confined to the winter rainfall area from Springbok to Mossel Bay and further eastward along the coast to near Grahamstown, where it rains throughout the year (Buys, 2006).



It is important to emphasize that 6 species of the 14 attributed to the *capensis*-group (Fig. 10) were collected from *Echium plantagineum*, an alien plant introduced into South Africa from Europe after 1825 and now present in Western and Eastern Cape and in the temperate mountain areas of Free State, Lesotho and Kwazulu-Natal, with some reports from southern Mpumalanga (cf. Retief & Van Wyk, 1998). From a systematic point of view, the genus *Echium* is a sister-group of *Lobostemon* (Böhle et al., 1996), so the host-plant shift from *Lobostemon* to *Echium* observed in some species of the *capensis*-group could have easily occurred. However, in our opinion, this ecological event could dramatically alter the autecology and evolutionary mechanisms of the species involved (Biondi & D'Alessandro, 2008). The presence of *E. plantagineum* in South Africa represents, in fact, a new “shared” trophic resource for the sympatric species of the *capensis*-group and, simultaneously, an unexpected connection among allopatric species as consequence of the easy spread of this invasive plant. On the basis of other analogous adaptive processes observed in native species in response to the introduction of invasive plants (Mooney & Cleland, 2001; Strauss et al., 2006), it is possible that unexpected evolutionary events could result in several different scenarios: (1) catalyze the local breakdown of reproductive isolation between native sympatric parent species; (2) bring into contact parent allopatric species and contribute to the reinforcement (or deletion) of reproductive isolating mechanisms; and (3) promote speciation by hybridization as an adaptive response of two or more native species to the new host-plant, as observed in species of the genus *Rhagoletis* Loew (Diptera Tephritidae) in testing invasive plants of *Lonicera* sp. (Caprifoliaceae) in North America (Schwarz et al., 2005, 2007).

With the knowledge presently available, it is impossible to evaluate which scenario among those listed above may play the most significant role in determining the high rate of species diversification within the *capensis*-group. Only further analyses focused on phylogeography by mean biomolecular analyses (*e.g.* coalescent simulation, biomolecular clock) may help clarify the paleobiogeography of the *capensis* species-group.

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