Blister Beetles (Coleoptera: Meloidae) in Nahavand County (Hamedan Province, Iran) and Their Ecological Relationship to Other Coleopteran Families

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ABSTRACT

Field collection in Nahavand county (Hamedan Province, Iran) revealed 9 blister beetle (Col. Meloidae) species from three different tribes of subfamily Meloinae. In tribe Mylabrini, Mylabris impressa Chevrolat 1837, Mylabris schreibersi Reiche 1865, Mylabris variabilis (Pallas, 1781), Mylabris guerini Chevrolat 1837, Lydoceras bilineatus Thomas 1897 and Croscherichia spp. Pardo Alcaide identified; whereas in tribe Lyttini Alosimus smyrnensis (Maran 1942) and Muzimes iranicus (Maran 1942) found. Another species was Calydos alloushei Kaszab 1960 of tribe Eupomphini. Two records of Mylabris impressa and Mylabris schreibersi are quite new for Iranian fauna. There are some interesting mimicry rings between meloid species and 8 species of other coleopteran families which indicates a remarkable Müllerian mimicry. Mimics of the following families have taken advantage of Meloid aposematism towards a better natural fitness: Cerambycidae, Cleridae, Pedilidae, Melyridae, Chrysomelidae, Cantharidae and Cicindelidae. Canthariphily of families Chrysomelidae, Cantharidae and Cerambycidae are new reports which have never been shown elsewhere.

INTRODUCTION

Blister beetle is a common name for members of family Meloidae (Order Coleoptera), whose adults are often found on flowers. They are soft bodied insects which are generally elongate (10-20 mm) and pronotum is usually narrower than the base of elytra. Elytra have very different colourful patterns which make their fast identification a hard task. It is markedly constricted at postocciput to form a narrow neck. Antennae with 11 antennomeres, reduced to 7-10 in tribes Mylabrini and Cerocomini. Abdomen soft with 6 visible sterna. Male genitalia with aedeagus elongate, either with 1-2 distal dorsal hooks and 1 ventral endophallic hook. Parameres fused at base only. Phallobase large. Female genitalia short, lacking long membranous tube-like ovipositor (1).

Meloids with about 3000 species in 120 genera (8) are widespread throughout the world except for New Zealand and the Antarctic and their diversity is greatest in arid or semiarid regions (1). Some groups are phytophagous and feed on leaves and flowers of several families of plants, particularly Compositae, Astraceae, Leguminosae, Solanaceae and Umbliferae, whereas larval instars are parasite and feed on the provisions and immature stages of bees and in subfamilies Epicautini and Mylabrini, the eggs of grasshoppers. Larvae of meloidae differ from those of most other Tenebrionoidea in lacking a mola and urogomphi. Larval development is hypermetamorphic with the various instars differing considerably in morphology and behaviour.

Faunestic studies have been accomplished for North America (20), West Indies (25) and Mediterranian region (4), but the meloid fauna of Iran has been quite poorly known. The first report on Iranian fauna reflected in Redtenbacher article (23). Several publications by Z. Kaszab in 1950s and 1960s (13) have substantially contributed to our understanding of meloids in

Iran. The last research on Iranian meloids performed by Axentiev (2).

The hemolymph and tissues of all developmental stages of meloid beetles contain a vesicating substance called Cantharidin. This defensive chemical is commonly released through reflex bleeding when adult beetles are disturbed (1, 5, 8, 9, 27). The present study achieved because of some reports on blistering problems among human poulation and also shortage of information in western Iran. This article first indicates meloid diversity in Nahavand county and then clarifies some interesting ecological relationship between members of this family and some other coleopteran families.

MATERIALS AND METHODS

Nahavand county (Hamedan Province) is an agricultural region, located in the south of Hamedan city in the latitude of 34,13 N and longitude of 48,21 E and enjoys mild summers whilst winters are usually cold. This county is also a mountainous region with plenty of rivers, streams and ponds. Most of the land is under cultivation and the rest covered by wild vegetation.

The region was three times visited in May, June and July 2001 and 273 specimens were totally collected which later pinned, labelled and preserved for further research. Adult of meloids are usually found on the top of flowers; but considering their aggregation tendency, it is rather difficult to locate them in the field. The best time for collecting meloids was from 10:00 to 15:30 when weather was sunny and warmer than 30 °C. Samples were randomly taken via handcatch and the materials transferred to a killing jar.

During all trials in Nahavand county, the following districts were visited: Akbar- Abad, Saede Vaghas, Firoozan, Zappon,

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Sarkan, Gamasiab, Bayan, Ghal-e- Ghobad, Gian, Varzool, Gil Abad Hosein Abad and Mian Rood.

Keys to the Fauna D'Italia (4) were mostly used for identification of collected meloids. In order to confirm the species, materials were compared to the types in Hungarian National History Museum (HNHM), Budapest. Other coleopteran families were also identified by accessible keys (11, 24, 26, 28).

Cantharidin detection was performed by a Carlo Erba Vega Series2 GC-6000 gas chromatograph equipped with a HT8 (non-polar) fused silica capillary column (Chrompack, FT 0.25 , ID 0.32 mm, OD 0.43 mm) which in turn connected to a Finnigan MAT ITD (EI 70 ev) to quantify the detected amount. Total mass Spectra analysed by X-Calibor 2000 and base peaks were compared by NBS registry of mass spectral data bank. Method of chemical detection and quatitation has been precisely described by the authors in the article entitled 'Cantharidin Component of Iranian Blister Beetles (Col: Meloidae): What is the difference between Iranian & Exotic Species ?'.

RESULTS

Family Meloidae is divided into two subfamilies: Meloinae and Nemognathinae which most of meloids are placed in meloinae. Subfamily Meloinae includes 7 tribes (4), while collected materials belong to only 3 tribes. Identification of adults showed all collected specimens were from sub family Meloinae. Identified species and their tribes are listed below:

Tribe Mylabrini

1.		Mylabris	Eumylabris	impressa	Chevrolat
	1837				
2.		M. (s. str.) schreibersi l	Reiche 186	5
3.		M. (s. str.) variabilis (P	Pallas 1781)
4.		M. (s. str.) guerini Che	vrolat 1837	7
5.		Lydocera	s bilineatus T	homas 189	7
6.		Croscher	<i>ichia spp</i> . Par	do Alcaide	

Tribe Lyttini

- 1. Alosimus smyrnensis (Maran 1942)
- 2. Muzimes iranicus (Maran 1942)

Tibe Eupomphini

1. Calydos Calydabris alloushei Kaszab 1960

Regarding all published materials (2, 4, 10, 13, 14, 18, 19) and meloid collection in Hungarian Natural History Museum (HNHM), Budapest, *Mylabris impressa* and *Mylabris Schreibersi* should be new records for Iranian fauna.

Kaszab listed 70 species of Meloidae from Iran (13), but taking into account numerous earlier papers with separate new taxa and also our records, the fauna reaches a total of 142 known meloid species. However a considerable part of the fauna needs revision, because many forms seem to be synonyms or homonyms. That is why, the most recent classification by Bologna (4), followed here to prevent prior problems. Nevertheless, synonyms have been also indicated.

Synonyms

1.Mylabris impressa Zonabris vaucheri Zonabris aini Mylabris Mylabris impressa Mylabris Mesolaevigata impressa

2.Mylabris schreibersi Mylabris terminata

Mylabris terminata 3.Mvlabris variabilis

Mel e cichorii

Mel e variabilis

Zonabris variabilis

Mylabris lacera

Mylabris mutans

Mylabris hypocrita

Mylabris similaris

Zonabris erivanica

4. Mylabris guerini

Mylabris rubripennis

Mylabris variabilis

Mylabris quadripuctata

5.Alosimus smyrnensis

Alosimus syriacus Lydos syriacus

Oenas syriacus

Mel e syriacus

6.Muzimes iranicus

Micromerus iranicus

7.Calydos.

Caloenas

Mylabris

Zonabris

Oenas

Thirteen districts in Nahavand county visited; whereas meloids found only in 6 districts, which have been indicated in table 1. Meloids have aggregation tendency and usually concentrate in specific localities. Considering vegetation type, altitude, distance or environmental conditions, these localities have no significant difference from nearby ones; that is why, it still remained to be a question on the ecology of blister beetles.

Table 1. List of visited districts in Nahavand county, Hamedan

Province (Iran) and ones where any meloid has been found (May- July 2001)

Districts	Result
1. Akbar- Abad	-
2. Saede Vaghas	-
3. Firoozan	+
4. Zappon	-
5. Sarkan	+
6. Gamasiab	+
7. Bayan	-
8. Ghal-e- Ghobad	-
9. Gian	+
10. Varzool	-
11. Gil Abad	+
12. Hosein Abad	-
13. Mian Rood	+

Description of dentified Species

Mylabris impressa

Elitra convex with yellow- black pattern and short black hairs. Body opaque black, length 11-16 mm. Head is strongly divided with little parallel temples about 1/3 of longitudinal diameter of eyes. Forehead with one oblique depression towards base of the head and 2 oval red spots, convergent ahead. Frontal suture little arched but obvious. Labrum medium advanced and is nearly straight up to front margin. Antenna short (11 segmented), segments not compressed, uniform in length, the last five antennomeres are clubbed. Scutum semioval, smooth. Mesosternal suture a little bit visible. Elytral surface with fine and little deep punctuations. Elytra are not shining black with 3 rows of spots, rarely merging into narrow sinuate bands or rather reduced or even absent. Last abdominal sternite in male is visible with posterior margin closely and deeply reduced.

Mylabris schreibersi

Body parallel, little convex, dorsally black with yellowish elytra which punctuated by black patterns. Length 10-20 mm. Head strongly transverse with parallel temples and a little bit rounded off behind longitudinal eyes. Eyes of medium dimension and little convex. Forehead with two light oblique depressions towards base of the head and one round or cordiform red spot. Frontal suture quite obvious, labrum advanced. Antenna 11 segmented, black and long. Maxilla and maxillary palps not modified. Pronotum with small transverse anterior depression. Mesosternum lengthened posteriorly with small scutum, hairly in posterior. Mesopleuron is wide and little quadrate posteriorly, compressed on the scutum. Elytra with subrogose surface and pattern composed of 2 series of 2 punctiform spots and very narrow apical border, other spots larger. Patterns of elytra have not so much variation. Frequently, some spots can disappear in some populations or the two front and medium spots can join together to form sinus bands. Last abdominal sternite in male is visible with posterior margin to some extent deeply recorded. Aedeagus in lateral view with cylindrical and medium width with narrow parameres. Medium lobe small.

Mylabris variabilis

Body is elongate and black in colour, elytra is relatively convex. Elytra yellow with black bands. Punctuations of elytra decreased, elytra with many different patterns and colours but normally 3 black bands which the last not distinctly sinuate in the middle of anterior margin. The 1st and 2nd bands sometimes divided but rarely into four distinct spots. Length 8-20 mm. Head transverse, square shape; temples parallel, little rounded off behind, nearly 1/3 of longitudinal diameter of the eye. Forehead flat, little depressed in front towards the base of antennae with one median red spot. Frontal suture little obvious. Labrum advanced. Antenna black and long with 11 antennomeres. Pronotum long and wide, parallel in sides, without anterior depression; convex and little deep, punctuation similar to head but relatively stronger and more regular. Mesosternum less elongate in sides with long but not wide scutum; scutum with a posterior punctuated area. The last visible abdominal sternite of male with rather deep recording on the posterior margin. Aedeagus in lateral view with narrow parameres; terminal lobe increasingly slender, hooks of median lobe small, short and weakly curved but proximal one a little bit longer. Populations of western Iran indicate a more melanized elytra and black bands are less reduced.

Mylabris guerini

Body moderately convex and parallel, in black colour. Elytra yellow with black patterns, more or less punctuated. Pattern of elytra usually with 3 bands of which anterior and middle ones sometimes reduced to 4 points. Length 7-17 mm. Head transversal, squared; temples parallel and little rounded off behind, long but less than longitudinal diameter of eyes. Forehead flat with one red spot, sometimes changed into two convergent spots. Forehead with lots of deep points.Frontal suture obvious. Labrum advanced. Antenna black with 11 antennomeres. Maxilla and maxillary palps are normal. Pronotum a little bit wide and parallel in sides, but to some extent narrow at base; it is rugose with long, deep, converging foveate punctures which anterior transverse depression is distinct. Mesosternum extended in sides, with large scutum; scutum has a large punctuated area. Mesosternal suture reduced and hardly visible. The last visible abdominal sternite in males with tight and deep recording on the posterior margin. Aedeagus in lateral view with cylindrical parameres. Median lobe of parameres with 2 indents, strongly various. Parameres slightly widened laterally. Terminal lobe short and thick, weakly curved anteriorly; distal hook of median lobe short, almost perpendicular to axis of aedeagus.

Croscherichia

Outer spur of metatibiae longer than inner one, rather spatulate and transversally cut at apex. Mesosternum without middle scutum; mesosternal suture not very distinct and rather angulate. Body black or red, never metallic. Parameres of aedeagus elongate, narrow; almost subequal, far from apex, this latter subsquare and dorsally oblique. Length 7-23 mm.

Alosimus smyrnensis

Body black, covered with hairs; however the hairs of head and pronotum are longer than elytra. Pronotum red, subrounded, much wider than length, never with two black rounded spots. Elytra blue- green metallic. Length 6-20 mm. Head black without distinguished metallic reflection, with a small frontal red spot. Temples approximately 1 ½ of longitudinal diameter of eye, increased externally and rounded off behind with maximum width in front . Vertex wide and depressed. Antenna 11 segmented. Pronotum with a wide depression on the middle and the base. Pronotum punctuated with small but not deep spots. Aedeagus in dorsal view with fallobase and parameres. Paramer lobes covered by dispersed hairs. Females are different in antenna. Outer border of middle tibiae neither depressed nor densely setose; posterior femor larger than middle ones.

Muzimes iranicus

Pronotum subtrapezoidal, always red with two parallel black rounded spots in middle. Outer border of middle tibiae depressed and densely setose. Head red with rather extensive black colouring inferiorly and on frons. Elytra green or metallic blue. Legs red or apically dark. Length 17-38 mm.

Calydos alloshei

Body black, head with small, round front spots, tibia and tarsi, as well as the base of antennae brown, rarely the center of pronotum is darkly brownish-red.

Elytra yellow-red with black pattern: always with two rounded spots in the first quarter of elytra and a complete transverse band behind the center, which in the back is more strongly serrated than in front and finally the apex broadly black (Forma typica).

Head rounded, with densely black hairs, behind the eyes most broadly. The eyes are bean shape. Vertex into the center flattened or somewhat depressed. Neck oval, approximately in the center most broadly, to the rear less.

Integument appendices consist of obvious dots with smooth and shining area among the dots.

Antennae has not been thickened, the 3^{rd} antennomer stretched, two times longer than the 2^{nd} and more than 1.5 times longer than the 4^{th} . The 4^{th} and 5^{th} are of equal length. 6^{th} one somewhat longer and more broadly, 7^{th} even longer and more broadly, approximately triangular, Segments 9 and 10 as long

and broad as the 8^{th} one, but rather roundish, the last one is long and egg shape, nearly twice as long as the 10^{th} and the point sharply rounded off.

Scutellum broadly triangular. Elytra long and parallel, with traces of hardly recognizable longitudinal lines, very closely and finely dotted.

Last Abdominal sternite of the male simply visible.

Legs have long hairs, hairs of inside of the front tibia are yellow. Tarsi at the end with long setae. Tarsi of the front legs in males with densely yellow hairs. The 1st tarsal segment of the last pair of the legs not longer than claw. The claws are very characteristic, because the lower tooth is short and broad and also completely rounded. Length: 15-18.5 mm.



Calydos Calydabris alloshei

Croscherichia sp.

Alosimus smyrnensis



Lydoceras bilineatus



Mylabris guerini



Muzimes iranicus



Mylabris schreibersi

DISCUSSION

Apart from those meloid species precisely identified, there are still four other species which remained unknown. The first one is a *Mylabris* and the second is a *Onyctenus* species while the two others are very difficult to be identified. Since, there is only one available specimen of these four species, it is not reasonable to dissect them and go further. There is no record of genus *Onyctenus*, so regardless of forthcoming information, number of new records for Meloidae fauna of Iran will reach three. In genus *Croscherichia*, there are lots of complexities in

classification and nomenclature, which make two species of the genus difficult to be identified.

However the basic aim of our field trial was meloid collection, some other coleopteran specimens were also found. They were collected mostly because of considerable similarities between some of the meloids and non- meloid taxa. These taxa apparently indicate mimicry and it was not possible to differentiate them in the field. Eight species of 7 coleopteran families were precisely identified (3, 7, 11, 16, 17, 22, 28, 29, 30, 31, 32) which are listed as follow:

i. Family Cerambycidae Phymatodes testaceus

ii. Family Cleridae

Trichodes olivieri

Trichodes ephippiger

iii. Family Pedilidae

Pedilus sp.

Eurygenius sp.

4. Family Melyridae

Malachius bipustulatus

5. Family Chrysomelidae *Oulema melanopus*

6. Family Cantharidae *Cantharis sp.*

iv. Family Cicindelidae

There was only one species in family Cicindellidae which we haven't been able to identify it exactly. It was sent to British Natural History Museum (BNHM) for species determination. *Phymatodes testaceus* (Cerambycidae), *Pedilus sp.* & *Eurygenius sp.* (Pedilidae), *Oulema melanopus* (Chrysomelidae) and the Cicindelid specimen were found in natural habitats of the meloid species, *Alosimus smyrnensis*. All were collected in large number from noon to 17: 00 PM on different compositae

flowers. Interestingly, two species of family Cleridae, Trichodes olivieri and T. ephippiger were exactly found in the same habitats as the meloid species, Mylabris impressa. Both mentioned groups are very similar in size, elytral pattern and general colouration to blister beetles. Using of cantharidin contained hemolymph in meloids has already proved to be a potent deterring device against invasive arthropods (5, 6, 8, 9). Experiments by GC- MS revealed that all referred mimics had traces of cantharidin in their body. The quantity of cantharidin in mimics is not comparable to producing taxa; so they should be only canthariphilous insects, not producing ones (Unpublished data). All these data show an interesting ecological relationship between the two cantharidin producing insects (Alosimus smyrnensis and Mylabris impressa) and mentioned coleopteran species. Regarding the physical and chemical similarities, it is now clear that there is a Müllerian mimicry ring among these insects which provide them a natural fitness. Previous reports of *Pedilus* and *Trichodes* predation on blister beetles or melyrid attraction to cantharidin baits (12, 15) support our idea in canthariphily of these insects. Besides, origin of cantharidin in non- producing taxa will be better cleared. Canthariphily in Chrysomelidae, Cantharidae and Cerambycidae is a new report which has never been shown elsewhere.



Malachius bipustulatus



Pedilus sp.



Cantharis sp.



Trichodes ephippiger



Oulema melanopus



Trichodes olivieri



Phymatodes testaceus



Cicindellidae

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REFERENCES

- 1. Arnett RH, Thomas MC, Skelley PE and Frank JH (2002): American Beetles. CRC Press. Boca Raton, Florida. PP:861.
- 2. Axentiev SI (1985): Meloidae from Iran (Insecta: Coleoptera). Senkenbergiana Biol, 65(3/6):245-50.

- Cryptocephalinae (Coleopteres, Chrysomelidae). Nouv. Revue Ent, **9**:239-69.
- 4. Bologna MA(1991): Fauna D'Italia. Edizioni Calderini. Bologna, PP: 541.
- Carrel JE, McCairel MH, Slagle AJ, Doom JP, Brill J and McCormick JP (1993): Cantharidin Production in a Blister Beetle. Experientia, 49(2): 171-4.
- 6. Carrel JE and Eisner T (1974): Cantharidin: Potent Feeding Deterrent to Insects. Science, 183:755-6.
- 7. Cassala F(1976): Cntribution a la faune du Pakistan (Col: Cicindelidae). Ann Soc Ent Fr (N.S.), 12(19):75-81.
- 8. Dettner K, Bauer G and Vlkl W (1997): Vertical Food Web Interactions. Springer Verlag. Berlin.PP:390.
- Dixon AFG, Martin Smith M and Smith SJ (1963): Isolation of Cantharidin from Mel e proscarabeus. Canadian Pharmaceu J, 29:

- Dvorak M (1983): Drei neue Arten und einige Bemerkungen zur Familie Meloidae (Coleoptera). Acta Ent Bohemoslov, 80:441-50.
- Gerstmeier R (1998): Checkered Beetles; Illustrated Key to the Cleridae and Thanerocleridae of the Western Palaearctic. Margraf Verlag. Weirsheim. PP:241.
- Hemp C and Dettner K. (2001): Compilation of Canthariphilous Insects. Beitr Ent, 51(1):231-45.
- Kazsab Z (1968): Contribution a la faune de l'Iran (Coleopteres Meloidae). Ann Soc Ent Fr (N.S.), 4(3):749-76.
- Kaszab Z (1960): Die Arten und die Systematische Stellung der Meloiden Gattung Calydos. Acta Zool Hung, 6(1-2):125-34.
- LeSage L and Bousquet Y (1983): A New Record of Attacks by Pedilus (Pedilidae) on Mel e (Coleoptera: Meloidae). Ent News, 94(3):95-6.
 - Medvedev LN (1983): Chrysomelidae from Iran (Insecta: Coleoptera). Senckenberg Biol, 64:133-40.
- Medvedev LN (1970): Contribution a la faune de l'Iran. 20.
 Coleopteres Chrysomelidae. Ann Soc Ent Fr (N.S.). 6:999-1002.
- Mirzayans H (1970): Contribution a la Connaissance de la faune des Clerides et Meloides de l'Iran. Ent Phytopath. Appl, 29:25-37.
- Ozbek H and Szaloki D (1998): A Contribution to the Knowledge of the Meloidae (Coleoptera) Fauna of Turkey along with New Records. *Turk J Zool*, 22(1): 23-40.
- Pinto JD and Bologna MA (1999): The New World Genera of Meloidae (Coleoptera): A Key & Synopsis. J Natur His, 33: 569-620
- Prestwitch GD and Blomquist GJ(1987): Pheromone Biochemistry. Academic Press. Orlando.PP: 565.

- Rapilly M (1978): Contribution a la faune de l'Iran (Coleoptera: Chrysomelidae). Nouv. Revue Ent., 8:329-43.
- Redtenbacher L (1850): Über den charakter der Insekten- Fauna von Südpersien. Denkschr. Acad Wiss Wien, 1:42-53.
- Schaefer M (1992): Brohmer Fauna of Germany. Quelle & Meyer Verlag. Wiesbaden. PP:704.
- Selander RB and Bouseman JK. (1960): Meloid Beetles (Coleoptera) of the West Indies. Proceedings of the United States Natur Museum. 111:197-226.
- Hanneman HJ, Klausnitzer B and Senglaub K (2000): Stresemann Exkursionfauna von Deutschland. Spektrum Akademischer Verlag. Heidelberg.PP:959.
- 27. Towsend LH (2002): Blister Beetles in Alfalfa. University of Kentucky, College of Agriculture. http://www.uky.edu/Agriculture/Entomology/entfacts/fldcrops/ef10 2.htm.
- Trautner J (1987): Tiger Beetles & Ground Beetles; Illustrated Key to the Cicindelidae and Carabidae of Europe. Margraf Verlag. Aichtal, PP:488.
- Wittmar W (1986): Beitrag zur kenntis der Palaearktischen Fauna. Mitt. Ent Ges Basel, 36(3): 100-92.
- Wittmar W (1979):Beitrag zur kenntis der Palaearktischen Cantharidae Phengodidae und Malachiidae (Col.). Ent Basil, 4: 327-46.
- Wittmar W (1974): Beitrag zur kenntis der Palaearktischen Cantharidae und Malachiidae (Coleoptera). Fragm Ent, 10(1): 1-20.
- Wittmar W (1972): Zur kenntis der Cantharidae Irans. Verh. Naturforsch. Ges Basel, 82(2): 193-204.