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Genetics of oil beetles (*Meloe*, Coleoptera) *in silico*

A tribute to *Franz von Paula Schrank* [1747–1835] 1776

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Abstract – Oil beetles (genus *Meloe*, order Coleoptera) comprise over 150 species with 55 entries in GenBank to date. One of the first *Meloe* species was described by LINNÉ, K. [1707–1771] *M. proscarabaeus* (black oil beetle) applying the early theory of BAUHIN, C. [1560–1624] who suggested first the use of *binomial nomenclature* to describe plant and animal species. After LINNÉ, further *Meloe* species were described, *e.g., M. hungarus* identified by PAULA SCHRANK [1747–1835] 1776, working in city Selmecbánya, Hungarian Kingdom, Europe. Here we analyze sequences of DNA of mitogenomes (mtDNA), genes and proteins of *Meloe* species based on *in silico* data mining, sequence and cladogram analyses to reveal new phylogenetic and molecular relationships among and within *Meloe* species.

A protein cladogram of *NADH dehydrogenase subunit*5 (mtDNA, 577 aa) of *Meloe* species revealed that *M. proscarabaeus* shows the closest similarity to *M. poggii* at the highest bootstrap (100) level. In the analysis of complete mtDNA genomes (16.154 DNA bp each) the oil beetle species of the three main genera of *Meloe*, *Epicauta* and *Hycleus* were discriminated sharply at high (95-100) bootstrap levels which result may provide a direct marker for molecular identification of oil beetles. In the analysis of nuclear wingless gene (*wg*) sequences (514 DNA bp each), and cladogram analysis the two species of *M. proscarabaeus* and *Mylabris amorii* showed distinct clade, which indicated multifunctional roles of *wg* genes in oil beetles. The survey of a biochemical marker revealed that not only oil beetles but plants, *e.g.*, *Butea frondosa* (flame-of-the-forest) tropical tree (*Fabaceae*), contains *cantharidin* ($C_{10}H_{12}O_4$; MW: 196.2 g/mol) and a related compound *palasonin* (*i.e., demethylcantharidin*; $C_9H_{10}O_4$; MW: 182.17 g/mol) (https://pubchem.ncbi.nlm.nih.gov).

Keywords: oil beetles (*Meloe* ssp.), phylogenetic relationships, DNA and protein sequence alignments, cladogram analysis

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BACKGROUD

Oil beetles (*Meloe*) (Fig. 1) feed on plants (*i.e.,* phytophagous) mainly forbs, and when threatened they release yellow oily poisonous droplets of *hemolymph* from the joints of legs, neck, and antennae. These droplets contain a defensive strong smelling compound *cantharidin* (CTD), a *monoterpene anhydride* which is highly toxic to vertebrates causing skin blistering (*i.e.,* blister beetles) on the human skin (Chen *et al.,* 2022). The name was derived from the Greek word for beetle *kantharos*.

Blister beetles especially *Lytta vesicatoria* (*Eng.*, Spanish fly; *Hung.*, kőrisbogár) (Fig. 5/a) have been used medicinally in powdered or tincture forms in the Roman- and Middle Ages of Europe as diuretic and aphrodisiac. Recently it has also been used as an anti-cancer drug (McCormick and Carell, 1987; Kőmíves and Király, 2019; Ren and Kinghorn, 2021) (BEZSILLA L [1903–1983]; SZALKAY J [1904–1986], 1971); SZELÉNYI G [1904–1982]; MÓCZÁR L [1914–2015]; VAJON I [1929–2020]; VARGA Z [1939–]).

Size differences showed sexual dimorphism (Fig. 1/i) between males (♂) and females (♀) (Gyulai *et al.,* 1969, 1978).

Meloe populations have expanded in range for the last 50,000 years (Sánchez-Vialas, *et al.,* 2024), however, they are still absent from New Zealand (Di Giulio *et al.,* 2014).

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Meloe species live unique life cycles as the first developmental stage larvae (>1.5 mm) (*i.e.*, *triangulins* after the *Lat., triangulinus* – 'legs with three nails'; *Syn.*, *instar*) parasitize ('riding on') bee larvae of ground-nesting bees (for >90 days). It indicates the roles in the co-evolutionary and ecological consequences in *ecocycles* (Kaszab, 1983; Bologna and Pinto, 1998; Lückmann and Scharf, 2004; Háva, 2018). The life form (*i.e.,* larval *phoresy*) has a long archaeogenetical (Gyulai, 2011; Ali *et al.,* 2015) history (TUZSON J [1870–1943], ANDREÁNSZKY G [1895–1967]) of 98.79 ± 0.62 MYA (*In:* Poinar and Brown, 2020). The ecological life form of larval *phoresy* of *Meloe* species are similar to larvae of *Thrips* [JENSER G, 1931–2015] and *Varroa* which ride on honeybees (Borges, 2022).

After LINNÉ (1753) further *Meloe* species were identified, *e.g., M. hungarus* (Fig. 1/c) described by PAULA SCHRANK [1747–1835] (1776) working in the Hungarian Kingdom (www.irmng.org); *M. tuccius* ROSSI P [1738–1803] 1792; *M. brevicollis* (short-necked oil beetle) PANZER GWF [1755–1829] 1793; *M. rugosus* (rugged oil beetle) (Fig. 1/e) and *M. violaceus* (violet oil beetle) (Fig. 1/f) MARSHAM T [1748–1819] 1802; *M. americanus* (buttercup oil beetle) (Fig. 1/g) LEACH, WE [1791–1836] 1815; *M. strigulosus* MANNERHEIM CG [1797–1854] 1852; *M. mediterraneus* (NCBI:txid2781717; MÜLLER JG [1880–1964] 1925; and *M. schmidi* KASZAB Z [1915–1986] (1942).

New *Meloe* species of *M. kulabensis* from Tajikistan (Shapovalov, 2014), and *M. xuhaoi* with ten new species including *M. kaszabi* were described recently from China (Pan and Bologna, 2021); and *M. wrzecionkoi* from Hungary (Bubenik, 2023).

Species of *Lampromeloe* (*Meloe*) DONOVAN E [1768–1837] (1793), REITTER E [1845–1920] 1911); *Eurymeloe (Meloe) mediterraneus* MÜLLER JG [1880–1964] 1925; *Desertimeloe* (Kaszab, 1983); and *Berberomeloe* (Fig. 1/b) were taxonomically separated from genus *Meloe* (Pan and Bologna, 2021; Sánchez-Vialas *et al.,* 2024).

Hungarian early studies have reported 45 *Meloe* species KUTHY B [1873–1946] (1897); Ábrahám *et al.,* (2014) (*In*: KASZAB Z [1915–1986] (1942) with further reports of ÁBRAHÁM A [1893–1989], KOLOSVÁRY G [1901–1968].

In Ireland/Eire 3 *Meloidae* species of the total 2,154 Coleoptera have been registered (https://en.wikipedia.org/wiki/List_of_beetles_of_Ireland). In the UK 11 *Meloidae* species live of the total 4,034 Coleoptera (https://coleoptera.org.uk/family/meloidae).

In Hungary twelve *Meloe* species have been protected of the of the total 6,350 Coleoptera species (Merkl and Vig, 2011; SZALÓKI, D. information): *M. autumnalis* (*Hung.,* őszi nünüke), *M. brevicollis* (tar n.), *M. cicatricosus* (óriás n.), *M. decorus* (díszes n.), *M. hungarus* (magyar n.) (Fig. 1/c), *M. mediterraneus* (déli n.), *M. rufiventris* (vöröshasú n.), *M. rugosus* (ráncos n.) (Fig. 1/e), *M. scabriusculus* (érdes n.), *M. tuccius* (gödörkés n.), *M. uralensis* (urális n.) and *M. variegatus* (pompás n.) (Fig. 1/d) (https://www.rovartani.hu).

Here we survey the genetic dynamics of *Meloe* species to add further molecular data to confirm the morphological based species borders. Species boundaries of oil beetles are fundamentally defined by distinct morphological differences (*e.g.*, thorax shape, antennae features, size, and color) which are tightly linked to their specialized, parasitic ecological roles involving specific ground-nesting bee hosts. This relationship is a classic example of co-evolution where both the oil beetles and the host bee species have developed reciprocal adaptations (Poinar and Brown, 2020).

Figure 1. Samples of female *Meloe* species - except *(f)* (>35 mm): *(a) M. proscarabaeus* (black oil beetle) (LINNÉ, 1758); *(b) M. (Berberomeloe) majalis* (LINNÉ, 1758); *(c) *M. hungarus* (PAULA SCHRANK, 1776; *(d) Meloe (Lampromeloe) variegatus* (DONOVAN, 1793); *(e) M. rugosus* (rugged oil beetle) (MARSHAM, 1802); *(f) M. violaceus* (violet oil beetle) (MARSHAM, 1802); *(g) M. americanus* (buttercup oil beetle) (ELFORD, 1815); and *(h) M. cavensis* (PETAGNA, 1819). *(i)* The size comparison of male (♂, 21 mm) and female (♀, 31 mm) *M. violaceus* with the bend on kinked antennae of males (♂) as the part of sexual dimorphism are indicated with arrows (*Photo* MAKAROV, K.B).

METHODOLOGY

Illustrations of significant *Meloe* species (Fig. 1, 2) were collected from web sites of:
https://portal.nature.cz/w/druh-6953#/;
https://www.itis.gov;
https://www.enfo.hu/index.php/node/7785;
https://doi.org/10.15468/nu60xi;
https://www.gbif.org/species/6953101;
https://www.kaefer-der-welt.de/artenliste.htm (*Photo, Schmidt, U.*);
http://www.meloidae.com/en/tags/hungary/;
https://www.zin.ru/Animalia/Coleoptera/rus/melvi2km.htm;
https://www.monaconatureencyclopedia.com
https://bugguide.net/node/view/1610018

Sequences of mitogenomes (mtDNA), genes and proteins were downloaded from the NCBI server (www.ncbi.nlm.nih.gov).

Protein sequences were also analyzed at Protein Data Bank (EMBL-EBI, https://www.ebi.ac.uk) and UniProt (https://www.uniprot.org). Sequences were aligned using the computer program BioEdit (Hall, 1999).

Neighbor-Joining (NJ) cladograms and statistical bootstrap analyses (x1000 replicates) were carried out by MEGA7 computer program (Kumar *et al.,* 2016) following the linear steps of the programs (Malone *et al.,* 1992; Bittsánszky *et al*., 2016; Tóth *et al.*, 2007; Gyulai *et al.,* 2022, 2025; Szabó *et al.,* 2023).

No nomenclature debates (Henderson and Henderson, 1963; Simoncsics, 2017) are discussed.

RESULTS and DISCUSSION

NADH dehydrogenase subunit-5 – Protein sequence analysis

For sequence analysis of protein the *NADH dehydrogenase subunit*-5 (mitochondrion; 577 amino acids, aa) (Du *et al.*, 2015) was selected. The analyzed cladogram showed two main branches of *Meloe* species which showed the closest relationships between *M. proscarabaeus* (▲) and *M. poggii* (▼) at maximum (100) bootstrap level (Fig. 2).

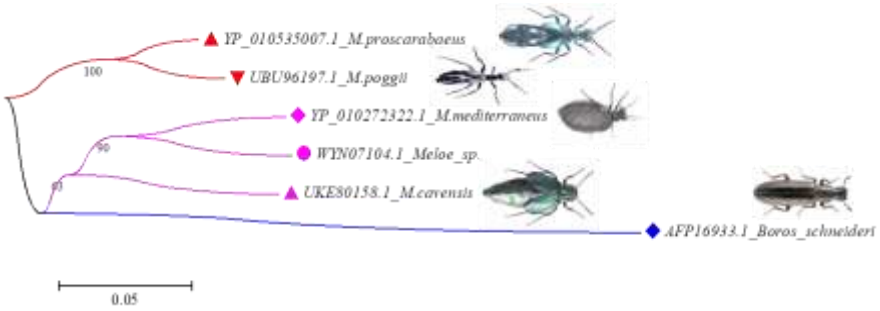


Figure 2. Protein cladogram (NJ) of *NADH dehydrogenase subunit*5 (mitochondrion, 577 aa) of *Meloe* species. The beetle *Boros schneideri* was used as an outgroup (conifer bark beetle; *Boridae*, Coleoptera; described by PANZER, GWF [1755–1829], 1796). The NCBI accession numbers, Latin names, bootstrap analysis (63–100) (x1.000 replicates), and the unit of genetic distance (0.05) are indicated.

Mitochondrial DNA – Sequence analysis

Mitogenome (*i.e.,* mitochondrial DNA, mtDNA), is located within the cell organelles called mitochondria (organelle # >1.000 per cell) which shows maternal inheritance (*i.e.,* sperm cells do not carry mitochondria into the egg cells as the cytoplasm of sperm cells remain excluded from the egg cell membrane and only the nucleus of the sperm cell penetrates the egg cell). Consequently, maternal inheritance, particularly of mitochondrial DNA (mtDNA) is highly useful for studying phylogenetic and species evolution (Sikes, 2001; Wells, 2002; Du *et al*., 2015; Zhou *et al*., 2021).

Like the short animal mitogenomes (*e.g.,* human 16,569 bp mtDNA, NCBI# NC_01292) compared to the huge (>10^6 bp) plant mitogenomes (Alverson *et al.,* 2010) the mtDNA of insects also show short mitogenome length. Here we compared complete mitogenomes (Fig. 3) of *Meloe proscarabaeus* (15,653 bp DNA, NCBI# NC_067881), *M. poggii* (16,626 bp DNA; NCBI# MW476520) (Zhou *et al*., 2021), and *M. mediterraneus* (15,130 bp DNA; NCBI# NC_060769) with outgroups of *Epicauta* (Du *et al*., 2015; Liu *et al.,* 2020) and *Hycleus* (*Syn., Mylabris / Meloe*) species to reveal phylogenetic relationships (Sánchez-Vialas *et al.,* 2024). The cladogram separated the three main clades of genera *Meloe* (> 150 species), *Epicauta* (> 360 species) and *Hycleus* (> 400 species) at high bootstrap levels (Fig. 4). Mitogenomes of the three *Meloe* species showed one clade (Fig. 4) similar to the protein cladogram of a single gene sequence analysis of *NADH dehydrogenase subunit*-5 (Fig. 3).

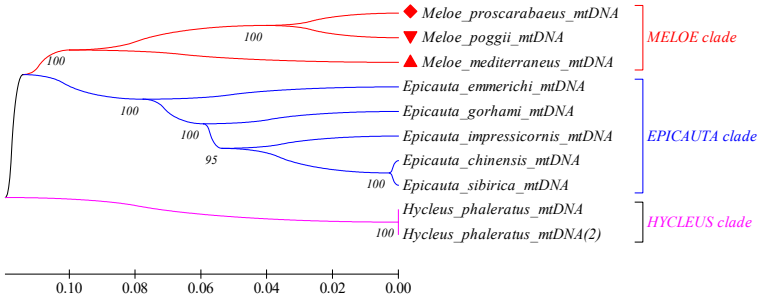


Figure 3. Complete mtDNA cladogram (NJ, Linearized) of ten genomes of *Meloe–Epicauta–Hycleus* species following sequence alignments (BioEdit, Hall, 1999). Lengths of sequences were chosen to the same length 16,154 bp DNA each. Bootstrap (93–100) analysis (x1.000 replicates), which provided the numbers of DNA bp changes along a 100 bp stretch are indicated. The cladogram was edited by MEGA7 computer program (Kumar *et al.,* 2016). Sequence ID#s are NC_060769.1; NC_067881.1; MW476520.1; NC_084326.1; NC_029192.1; NC_045246.1; NC_036042.1; MF491389.1; NC_036045.1; NC_068578.1.

Unlike the study of two nuclear and two mtDNA gene sequences reported by Sánchez-Vialas *et al.* (2024) the complete mtDNA genome analysis here reveled that the three *Meloe* species *M. proscarabaeus, M. poggii* and *M. mediterraneus* were separated from *Epicauta* and *Hycleus* clades at the highest (100) bootstrap level (Fig. 3)

Wingless genes *(wg)* – Sequence analysis

Similar to all *Diptera* species (flies, mosquito, *Drosophila*) *Meloe* species also have a single pair of fore wings without hind wings and have lost the ability to fly (Fig. 1).

A group of responsible wingless genes (*wg*) were first identified in fruit flies *Drosophila* (Klingensmith and Nusse, 1994). The protein of winglessness (WNT) of the fruit fly (*Drosophila melanogaster*) was found to consist 468 aa (51,986 Da) with functions as a ligand for members of the frizzled family of seven transmembrane receptors (UniProt.org, P09615 WNTG_DROME, PMID:11532397, PMID:19619488; Blum *et al.,* 2025).

The name WNT is derived from the names for the highly conserved *Wingless* and *Int*-1 genes (Nusse *et al.,* 1991; https://www.genecards.org).

Gene orthologs of *Drosophyla wnt* genes have been described in *Homo sapiens* (*wnt*-1 to *wnt*-16 isoforms), *Mus musculus* (*wnt*1), *Rattus norvegicus* (*wnt*1), *Xenopus tropicalis* (*wnt*1), *Danio rerio* (*wnt*1), and *Caenorhabditis elegans* (*cwn*-1, *egl*-20). All these genes from different species have evolved from a common ancestral gene through the speciation events (UniProt.org, P09615). Genomes of numerous insects of ants, wasps (Fig. 4), bees, sawfly, bumblebees, Apollo butterfly, cotton bollworm - carry active or inactive *wg* genes (NCBI).

Figure 4. Females of wingless wasp (*Dasymutilla occidentalis*) (10-15 mm) has no wings, a mimicry with resemblance to ant (*Syn*., 'velvet ant'). (*Photo:* G.Zs. Gyulai, AL, Alabama, USA).

Thrips species of Thysanoptera also developed the wingless form. Samples of winged and wingless ants (*Formica ssp*) ANDRÁSFALVY A [1929–2022] indicate the possibility of activation *vs*. deactivation of *wg* genes. Recently, homologs of *wg* and *wing* genes were found to contribute in the development of horns of horn beetles (Hu *et al*., 2019).

In the current study, we compared the sequences (NCBI) of *wg* genes (Hatini *et al*., 2000) and showed the closest distance between *M. tuccia* and *M. mediterraneus* at high bootstrap (x1.000) level (95) (Fig. 5).

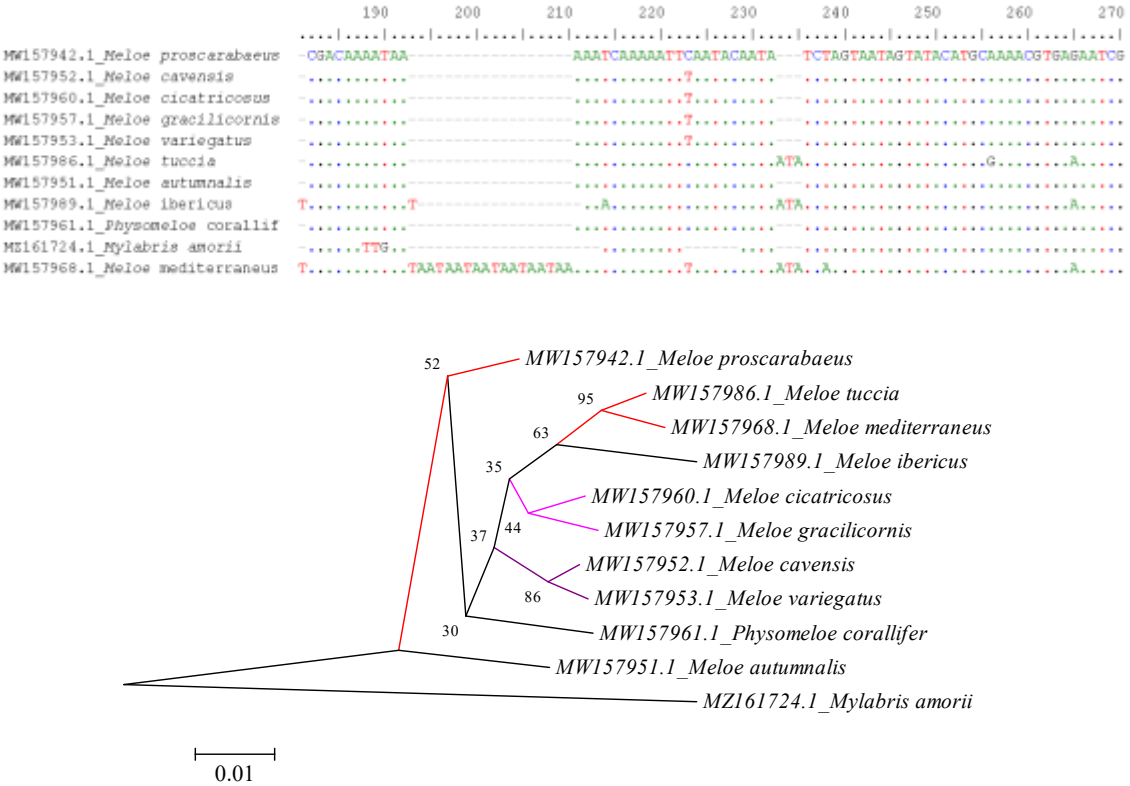
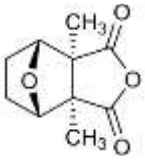


Figure 5. Samples of a stretch (181 to 270 DNA nt) of aligned wingless (*wg*) gene sequences of *Meloe* and related species (*top*), and NJ cladogram of the wingless (*wg*) genes (chosen to the same length 514 bp) (*bottom*). Consensus DNA nucleotides (dots), changes and indels of DNA (top), and taxonomic names, sequence ID#s, bootstrap values (x1.000 replicates) and the unit of genetic distance (0.01) which indicates the numbers of bp-changes along a 100 bp DNA are indicated (*bottom*).

Cantharidin (CTD; $C_{10}H_{12}O_4$) production of oil beetles



Oil beetles produce a strong smelling compound *cantharidin*. Similar to *Lytta vesicatoria* (Fig. 6/a) the Chinese blister beetle (*Mylabris phalerata; Syn., Hycleus phaleratus,* [Pallas, 1781]) (*Meloidae*) has been also used in traditional Chinese medication to treat cancer for over 2000 years. The bee-eating beetle (*Trichodes apiarius*) (*Hung*., méhészbogár) (Fig. 6/b) also produces *cantharidin* which showed antitumor activity in the human body (Ren and Kinghorn, 2021).

Genes related to CTD biosynthesis revealed that the *acetyl-CoA C-acetyltransferase* (*ACAT*; EC:2.3.1.9) gene which is conserved in Eukaryotes (NCBI# PLN02644; ID#: 2728096, 426 aa) shows central function in CTD biosynthesis (Wu *et al.,* 2023).

The *hydroxymethylglutaryl-CoA reductase* (*HMGR*; EC:1.1.1.34) activity showed positive correlations with CTD production.

The *hydroxymethylglutaryl-CoA synthase* (*HMGS*; EC:2.3.3.10) and i*sopentenyl-diphosphate delta-isomeras*e (*IDI*; EC:5.3.3.2) were found to be significantly up-regulated in male *Meloe* species compared to females (Huang *et. al*, 2024).

Hycleus cichorii and *H. phaleratus* (Fig. 3) (*Syn., Mylabris phalerata*) were compared to CTD production and male beetles were found to produce significantly higher amount then females which is a key example of sexual dimorphism in these insects (Wu *et al.,* 2023). Primers for qRT-PCR analysis of gene expression *3-Hydroxy-3-methylglutaryl CoA reductase* (*HMGR*) were provided to *Epicauta chinensis* (Jiang *et al*., 2017).

Gene copy numbers of NADP$^+$-dependent *farnesol dehydrogenase* (*FOHSDR*; EC:1.1.1.216) and *farnesyl diphosphate synthase* (*FDPS*; EC:2.5.1.1) showed the highest gene copy numbers in *Hycleus* species, significantly higher than in other non-*Meloidae* insects (Wu *et al.,* 2023).

Tropical tree *Butea frondosa* (flame-of-the-forest; *Fabaceae*) (Fig. 6/c) was found to produce *cantharidin*-related compound *palasonin* (*i.e., demethylcantharidin*) (Fietz *et al*., 2002; Tandon *et al*., 2003) and were used for medical purposes (Győrffy I [1880–1959], Greguss P [1889–1984], Soó R [1903–1980], Győrffy B [1911–1970], Simoncsics P [1918–2002], 2017), Szalai L [1920–1997], Suba J [1929–2024], Maróti I [1930–2024], Borhidi A [1932–], Gulyás S [1933–1996], Pócs T [1933–], Juhász L [1935–1993], Milkovits I [1937–], Juhász M [1938–2019], Lehoczki E [1941–2021], Dudits D [1943–], Kőmíves T [1944–], Heszky L [1945–], Balázs E [1948–], Podani J [1952–], Gyulai G [1953–], and Laskay G [1955–2014].

For mode-of-action analysis, *cantharidin* and related compound *(S)-palasonin* were found to act as inhibitor of enzyme *protein phosphatases*-1 (PP1- and 2A, PP2A) with serine/threonine-specificity, which showed inhibition to human cancer cell cytotoxicity (Ren and Kinghorn, 2021).

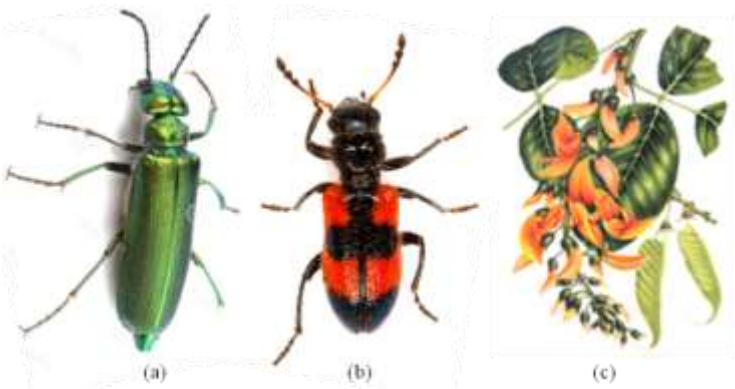


Figure 6. Cantharidin producing beetles (> 3-4 cm) and plant. *(a) Lytta vesicatoria* [*Meloidae*] (*Photo,* Käfer); *(b) Myrablis phalerata* [*Syn., Trichodes apiarius; Hycleus phaleratus*] (*Photo,* Salvator Vitanza); and *(c)* branch of *Butea frondosa* tree (*Fabaceae*) (*Source,* https://www.surfaceview.co.uk).

Conclusion

Here we analyzed sequences of mitogenomes (mtDNA), gene and protein sequences of *Meloe* species (Fig. 1) based on *in silico* GenBank data mining (www.ncbi.nlm.nih.gov) to reveal new phylogenetic and molecular relationships among and within *Meloe* species.

Similar to the single protein cladogram of *NADH dehydrogenase subunit*-5 (Fig. 2) the mitogenomes of the three *Meloe* species were grouped in one clade (Fig. 3), which indicated close evolutionary lineage of this species. However, like chloroplast genomes (Malone *et al.,* 1992) relocation of parts of mitogenomes into cell nuclear genomes is continuous and generally unidirectional process without back way gene flow (Butenko *et al.,* 2024).

The complete mitogenome (mtDNA) cladogram (Fig. 3) separated the three main oil beetles genera *Meloe, Epicauta* and *Hycleus*, which proved the morphological based systematics.

The sequence analyses of *wg* genes (Fig. 5) showed the closest sequence similarity between *M. tuccia* and *M. mediterraneus* (Fig. 2) at high bootstrap (x1.000) level (95) which would indicate close systematic relations between the two species (Fig. 5).

The synthesis of medicinally used *cantharidin* (Huang *et al.,* 2024) and related compound *palasonin* (*i.e., dimethyl-cantharidin*) of *Meloidae* species are not common among insects but universal as they are also expressed in plants (Fietz *et al.,* 2002; Safenraiter *et al*., 2024) such as in *Butea frondosa* (*Fabaceae*) tropical tree (Fig. 6), and would emphasize the importance of analysis ancient and current medicinal research of *cantharidin* and *palasonin*.

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