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Review Paper

Global zoogeography and systematic approaches of the blister beetles (Coleoptera: Meloidae): a bibliographic review

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Abstract

Blister beetles, or oil beetles, belong to the family Meloidae in order Coleoptera. They are cosmopolitan and distributed allover world except for New Zealand, Antarctica and some regions of Oceania. Some blister beetles are agricultural pests but all produce cantharidin which dangerously affect both animals, other than many canthariphilous insects, and man albeit it is used, in some parts of the world, to treat certain ailment cases such as cancer. The present work reviews the worldwide distribution of Meloidae throughout temperate, arid, sub-tropical and tropical regions, focusing on the most important identified subfamilies, tribes, genera and species in each region. Also, this review comprehensively highlights the systematic efforts in several parts of the world including various taxonomic methods and tools, especially the adult morphology, triungulin morphology, sexual and egg-laying behavioural patterns, adult anatomy and molecular data which have been recently used to disclose some elusory systematic problems.

Keywords: Meloinae, Eleticinae, Tetraonycinae, Lyttinae, Nemognathinae, phylogeny, morphology, anatomy, triungulins.

Introduction

The patterns of the past, present, and future distribution of animals in nature and the processes that regulate these distributions are concerns of zoogeography [1,2]. Also, it provides the basis for environmental protection and resource management [3]. Careful and accurate identification and classification of living organisms are of vital importance [4]. Without taxonomy, we could not begin to understand biodiversity and the related issue of conservation [5]. As Kapoor [4] pointed out, taxonomy is essential in theoretical and applied biology (agriculture and forestry, biological control, public health, wild life management, environmental problems, soil fertility, etc.).

The order Coleoptera includes more species than any other order, constituting almost 25% of all known life-forms [6]. About 40% of all described insect species are beetles (about 400,000 species [7], and new species are discovered frequently. Some estimates put the total number of species, described and undescribed, at as high as 100 million, but a figure of 1 million is more widely accepted [8]. Family Meloidae (Coleoptera, Polyphaga, Tenebrionoidea) is widespread throughout the world except for New Zealand and Antarctic [9]. Diversity is greatest in arid and semiarid regions. Distribution of meloid genera over the different zoogeographical regions was indicated by Bologna [10, 11]. As reported few years ago, Meloidae contains more than 3000 species in 120 genera. They are distributed throughout the world except for New Zealand, the Antarctica and some regions of Oceania [9, 12]. They primarily occur in temperate steppic and arid regions, and in sub-tropical and tropical savannas or other open habitats [13]. Adult beetles can be recognized by characters such as soft

body, bright or dark colouration, rather elongate, head deflexed with narrow neck, pronotum not carinate at sides, heteromerous tarsi, smooth integument [9, 10,11, 14].

Not all species of blister beetles can be considered as agricultural pests. Mostly in the New World, all economic pests belonging to family Meloidae are species of *vittata* group (Meloinae: Epicautini) which are known as pests of garden and field crops [15] and cause economic damages to potato, tomato, alfalfa, soybeans, sugar beet, cotton and a variety of truck crops and garden vegetables [16]. Also, some meloid species had been recorded as agricultural pests in the Old World such as the black oil beetle *Meloe proscarabaeus* Linneus, which was recorded by Zimmermann [17] as a serious pest damaging fields of red clover in Germany. Adults of *M. proscarabaeus* had been observed grazing on the plant *Ranuchus* sp. in Cornwall [18] and feeding on leaves and flowers of faba bean, peas, alfalfa, Egyptian clover, onion in Egypt [19, 20] . From the medical point of view, the most important families within Coleoptera are Meloidae, Staphylinidae, Oedemeridae, Tenebrionidae and Dermestidae in addition to very little species in other families may be considered as medically important insects [21, 22, 23, 24]. The present work aims to review the zoogeographical distribution of the most known meloid species in the world and their systematics based on morphological, anatomical characters and behavioural patterns, as well as using DNA sequence data.

Distribution of Meloidae in the World

“Blister beetles”, or "Oil beetles", are classified in the family Meloidae. The family, with about 120 genera and 3000 species, represents a monophyletic, cosmopolitan family of phytophagous beetles, divided into four subfamilies. This family had complex hypermetabolic development connected to larval parasitism on Hymenoptera (Aculeata) and Orthoptera (Acridoidea), and for the production of cantharidin [25]. These insects, are commonly very heterogeneous from point of morphology and are virtually cosmopolitan, absent only from New Zealand, Antarctica and most Oceanian islands [26].

In the Old World

Bologna and Pinto [27], in their comprehensive work on this family Meloidae in the Old World, cited the faunistic studies of the family Meloidae as follows: (1) Oriental-India and Sri Lanka [28, 29]. (2) Afrotropical-S Africa [30, 31], Namibia [32], Angola [33], Madagascar [34], NE Africa [35,36,37], Guinean Region [38, 39, 40]. (3) Palaearctic-N Africa [41, 42, 43, 44], Eastern Mediterranean and Iran [45, 46, 47, 48, 49], Arabian Peninsula [50], Macaronesia [51], Iberian Peninsula [52, 53, 54], Crimea (Ukraine) [55], Armenia [56], Tadzhkistan [57], Tibet [58].

The Mediterranean and Saharan regions harbor a rich diversity of Meloidae at the generic and species levels. Several genera are endemic to one subregion or the other, particularly the Mediterranean, whereas others occur in both reflecting a biogeographic similarity due to Cenozoic events which affected both northern Africa and southern Europe [59, 60, 61, 62]. Aksentjev [63] reported new genera and species of Meloidae in Central Asia. Mohamedsaid [64] studied on the Malaysian blister beetles. In the Old World, the range of blister beetles of the genus *Meloe* extends without major gaps from Western Europe to Japan and south to the northern limits of the tropics. Within this area occur some 105 species, many of them wide ranging. Three species occur in the Oriental Region. The Ethiopian representation is better (15 species), but the range of the genus there is restricted [65].

However, special attention should be paid to meloid distribution according to the continents. In **Asia**, the Japanese insect collection in the National Natural Museum in Leiden (Netherland) contains *Epicauta gorhami* Marseul, *Meloe coarctatus* Motschulsky and *Meloe carvinus* Marseul] 66]. Also, *Meloe corvinus* Marseul, *Meloe lobata* Gebler, and some other blister beetles were reported in different parts of Japan (for review, see [67, 68, 69, 70, 71, 72]). Chinese Meloidae currently include 192 species and subspecies in 25 genera in 8 tribes. Zhang et al. [73] recorded 10 new species of Meloidae and revised 41 species in 5 genera in China. Huang et al. [74] studied the faunal composition of Meloidae in Xinjiang. A new species of genus *Epicauta* Dejean from Yunnan in China, namely, *Epicauta cryptogramaca* was reported by Yang and Ren [75]. The blister beetle *Hycleus tekkensis tekkensis* (Heyden) was recorded for the first time as a species of the genus *Hycleus* in Xinjiang [76]. A newly recorded genus of Meloidae and a new recorded species *Rhampholyssa steveni* (Fischer) were recorded from China for the first time [77].

Depending on the "Atlas of blister beetles (Meloidae) of Russia", there are many species such as *Meloe* (*Proscarabaeus*] *proscarabaeus* Linneus, *Meloe violaceus* Marsham, *Meloe erythrocnemus* Pallas, *Cerocoma schefferi* (Linnaeus), *Cerocoma schreberi* (Fabricius), *Stenodera caucasica* (Pallas], *Alosimus syriacus* (Linnaeus), *Lytta vesicatoria* (Linnaeus), *Apalus* (=*Hapalus*) *bimaculatus* (Linnaeus), *Epicauta erythrocephala* (Pallas), *Mylabris speciosa* Pallas. Also, Tshernyshev and Axentiev [78] studied the blister-beetles of Mongolia. According to the catalogue of Silfverberg [79], *Meloe brevicollis* Panzer has been recorded in Belarus [80]. For the northern territory of the former East Prussia, this species has been reported from Trempen, Kaliningrad [81]. It is rare species in the region, known from the western part of the Sambian peninsula only. Pripisnova [57, 82] studied the meloid fauna from the Tadzhikistan. The insect fauna of Khorezm and Karakalpakstan (Uzbekistan) include 5 meloid species, such as *Mylabris pusilla* Olivier [83]. The blister beetles *Mylabris biiiiiguttata* Gelber, *Mylabris frolovi* Germar and *Mylabris schrenki* Gebler were reported in the Khorezm region and Karakalpakstan [84]. The Kyrgyzstan meloid fauna was studied and new species were discovered [85]. For some information about the meloid species in Siberia, see Cherepanov [86, 87]. It is important to mention that the genus *Euzonitis* Semenov within the tribe Nemognathini is represented by eighteen species distributed from Madeira to central Asia as far as Mongolia [27]. Concerning the blister beetle *E. erythrocephala*, it is known from Caucasus, and South Russia, Uzbekistan and Kazakstan. This species is apparently new to the fauna of Uighur Hi [88], while the blister beetle *Epicauta waterhousei* (Haag-Rutenberg) occurs in Thailand, Taiwan, etc. In Thailand, it is known in Central and Northeast provinces.

Near the Asia, Blair [89] reported the blister beetle Zonitis oceanica Blair as a new species of Truk Islands, Dublon Island, Marianas Islands and Guam Island. The blister beetle *Glipa tricolor* (Wiedem) was of wide distribution in Sikkim, Assam, Burma, Indo-China, Hainan Island, Siam, Malaysian Islands, Sumatra, Java, Borneo, Philippine Islands, Celebes and Sulawesi. The blister beetle *Mordellistena glipodoides* Blair distributed in Kusaie Island, Mount Matante, it was previously known only from South India, Sri Lanka, Singapore, and Borneo.

Anand [90] reported a new species of the genus *Psaldolytta* in India. The black oil beetle (or European oil beetle) *M. proscarabaeus* and the violet oil beetle *M. violaceus* were discovered with bees as a new record and adults of them were collected from Himalayan region [91] and Anand [92] recorded two new species of *Mylabris* Fabricius. In Sri Lanka, distribution of 15 species in 7 genera of Meloidae were cited [28]. The *Mylabris* spp. were recorded among 12 species belonging to 5 different families of beetles from the Sipna Range, and Melghat Tiger Reserve, India [93].

The Meloidae fauna in Iran includes more than 180 species, some of which were described in a large number of papers conducted by Kaszab [34, 94, 95, 96] and by Aksentjev [97]. Serri [98] studied 5 species as firstly recorded in Iranian fauna, some of them are: *Alosimus reitterianus* (Semenov) and *Cerocoma turcica* Pardo Alcaide. Nikbaktzadeh and Tirgari [99] carried out a field study in Nahavand county recording 9 blister beetle species of three different tribes of subfamily Meloinae. A preliminary faunistic study on 15 families of Coleoptera occurring in some cotton fields in the northern parts of Iran was carried out (2008-2010) by Ghahari et al. [100]. The following meloid species were collected from the fields and surrounding grasslands: *Alosimus syriacus rauterbergi* (Reitter), *Apalus necydaleus* (Pallas), *Zonitis* (*Zonitis*) *flava* Fabricius.

In Arabia, Kaszab [50] studied the Meloidae of Saudi Arabia and provided a synopsis of the Arabian genera and species. Bologna and Turco [101] reported some Meloid species in the United Arab Emirates and provided an updated Arabian checklist. Some meloid beetles had been reported from United Arab Emirates (for review, see [102]).

In **Africa**, Bologna [37] studied the meloid fauna in Somalia. Bologna [103] described a new Eleticinae genus from Ethiopia. The meloid beetle *Lytta coeruleata* Fairmaire was recorded from Bezà Mahafaly, Madagascar [104]. In Africa, also, Gahukar et al. [105] reported the geographic distribution, host plants and seasonal fluctuations of meloids in Mali and Senegal. Bologna [40] reported some Meloid species in Sierra Leone. Pardo Alcaide [106] reported meloid beetles in Chad. Most numerous blister beetles such as *Mylabris oculata* Thunberg, *Mylabris lunata* (Pallas), and *Cyaneolytta subcoriacea* Maklin were found in South Africa[107]. Moor [31] recorded some meloid species in Botswana. Bologna [32] studied the biodiversity of the Meloidae in Namibia. Bologna [108] recorded *Australytta*, as a new blister beetle genus and Bologna and Pitzalis [109] studied the taxonomy of *Iselma* Kaszab, as an ignored meloid genus endemic to South Africa. In South Africa, also, Mathews et al. [110] recorded some

meloid beetles on pigeonpea; Picker et al. [111] provided a field guide to insects including Meloidae; the endemic diversification of the Cape zone fauna and the phylogenetic relationships among the 30 species of the blister beetle genus *Iselma* are investigated by Pitzalis and Bologna [112]. However, the presence of the tribe Morphozonitini (Eleticinae) was documented and three new taxa were described in Namibia, Angola, Kenya [113].

In Libya, some meloid beetles were reported [114-118]. Also, light trap was used to collect some meloids in Tripoli [119]. Bologna [62,120] published an annotated catalogue of Meloidae which contains 64 species belonging to 17 genera. Some meloid beetles were cited in Tunisia [114,121]. Some meloid beetles in Sahara of Morocco were recorded [122,123]. The blister beetles, *Mylabris oleae* Castelnau and *Mylabris calida* Pallas, in the high steppic plain of Tlemcen (Algeria) was reported [124,125]. In Egypt, several meloid species and other families of Coleoptera were recorded [44]. The first reference reporting *M. proscarabaeus*, as an agricultural pest attacking faba bean, peas, alfalfa, onion and wild weeds was Ali et al. [19, 20] in El-Farafra oasis. Thereafter, seven species in the genus *Meloe* was reported in Egypt [126]. As previously mentioned, *Euzonitis*, is represented by eighteen species distributed from Madeira, the Maghreb and the Iberian Peninsula, to central Asia as far as Mongolia [27].

In the Mediterranean region, some blister beetles of the genus *Leptopalpus* are distributed in Europe and northern Africa. The geographic distribution of *Meloe majalis* Linnaeus in the Mediterranean region (including Europe and North Africa) was discussed by Bologna [47]. The genus *Eurymeloe* focusing on the most of European, west Asiatic and Mediterranean species of the *Meloe rugosus* Marsham group [47]. In addition, the dispersal, dispersion and phoresy in blister beetles fauna of eastern Mediterranean and other islands had been discussed [127].

In **Europe**, 28 meloid species belonging to different genera were reported in Poland [128]. Because *M. proscarabaeus* in Austria has attracted the attention of some researchers, Klausnitzer and Rauch [129] reported some observations on triungulin larvae on a small Buddleja shrub in a garden at Innsbruck. Also, triungulins of *M. proscarabaeus*, *M. brevicollis* and *M. rugosus* had been studied in certain localities in Germany [130]. Some meloid beetles in the fauna of Greece were reported [48]. The blister beetle *Zonitis fernancastroi* Pardo Alcaide was recorded as a new species among the fauna of France [132]. Pardo Alcaide [123,133] studied the Meloidae in Spain. In a valuable review of Anthicidae or ant-like flower beetles of the UK, Ireland and Channel Isles, some meloid species on which the cantharophilous species had reported feeding on their adult secretions [134]. In Czech Republic, *M. violaceus* was recorded from the top of Snezka Mountain (The Giant Mountains) [135]. Some meloid beetles were reported among the fauna of Italia [11, 41, 136- 138]. Until 2009, the recorded fauna of the Republic of Moldova contains 24 species belonging to two subfamilies: Meloinae and Zonitidinae. Those 24 meloid species were described for the first time in the fauna of the country [139] and were republished [140]. The family Meloidae in Moldova, also, has been mentioned in some papers with some ecological aspects [141-143]. Two new species in the republic fauna: *Meloe variegates* Donovan and *Oenas crassicornis* (Illiger) were firstly reported [144]. The blister beetle *Apalus bimaculatus* Laest inhabit sandy habitats and in Sweden it emerges as soon as the snow melts in spring, the adult activity period normally takes place from early March to the middle of April [145].

In the Iberian Peninsula, the faunistics and corology of Meloidae of the arid zones of the South Eastern region were studied [146]. Then, a contribution to the knowledge of Meloidae in the southern regions was conducted [147]. The known distribution of all 11 meloid species, depending on different collections from Andalusía, were expanded in Spain with a documentation of the first record of *Mylabris* (s.str.) *variabilis* (Pallas) from Andalusía and of *Meloe* (*Eurymeloe*) *ganglbauery* Apfelbeck from the peninsula [146, 147]. In the present century, the genus *Hycleus*, included in the tribe Mylabrini, was represented by five species. Trotta-Moreu and García-París [148] actualized the Iberian geographic range of each species. The geographic distribution of two species in the tribe Cercocomini was discussed in study on the faunistics of the same tribe in Catalonia (NE of Iberian peninsula) [149]. Also, 22 new records were reported [150]. However, the tribe was represented in the Iberia by two species of the genus *Cerocoma* Geoffroy: *Cerocoma (Cerocoma) schaefferi* (Linnaeus) and *Cerocoma* (*Metacerocoma*) *schreberi* Fabricius. The genus *Euzonitis*, within the tribe Nemognathini Lacordaire, is represented by eighteen species distributed in the Iberian Peninsula [27]. García-París et al. [151] revised the geographic distribution of the Iberian species of the tribe Lyttini in six species belonging to five genera: *Berberomeloe, Lagorina, Lytta, Oenas*, and *Physomeloe*. A new record of *Zonitis fernancastroi* was provided for the south of the Iberia, more precisely from Nerja (Province of Malaga), thus expanding the known Iberian range of this taxon. Data concerning the habitat and

trophic habits of this species in the recorded locality were presented [152]. In the same year, also, information about the distribution of 52 species of Iberian meloids was provided [153]. The geographic range of *Mylabris* (*Micrabris*) *beauregardi* Gorriz Munoz and *Mylabris* (*Mylabris*) *maculosopunctata* Graells was discussed in the Iberian Peninsula [154].

In Turkey, the Meloidae fauna had been studied by some scientists [45, 46, 155-160]. As a Turkish scientist, Öncüer [161] listed many species of Meloidae occurring mostly in western Anatolia in his catalogue and indicated most of them as new records for the Turkish fauna. However, all of them had been already reported before [46]. The first comprehensive zoogeographical analysis of Meloidae included 56 species in 12 genera and newly recorded some species in the genus *Mylabris* [46]. During the period from 1970s up to 1996, Ozbek and Szaloki [49] conducted a faunistic study of the Meloidae fauna including 147 species of 17 genera in two subfamilies, among which the blister beetles *A. reitterianus*, *Coryna confluens* Reiche, *Mylabris cingulata* Faldermann, *Mylabris colligata* Redtenbacher, *Mylabris furcimacula* Sumakov, were recorded. The blister beetle *Teratolytta kulzeri* was collected from Saruhan Mount [162].

In the New World

In general, faunistic studies on Meloidae of **North America** had been carried out [163]. Kerr and Packer [164] collected species distribution data on a North American beetle genus, *Epicauta* and tested several major diversity hypotheses. They concluded that the species richness-energy hypothesis currently provides a better overall explanation for *Epicauta* species richness patterns in North America than other major diversity hypotheses. The genus is distributed broadly, and may be found on all continents except Australia [165]. In Canada, the striped blister beetle *Epicauta vittata* (Fabricius) from Quebec and Ontario was reported [166]. Nineteen new species records for the faunal list of Coleoptera in New Brunswick, among which three species of Meloidae, *Epicauta pestifera* Werner, *Lytta sayi* LeConte, and *Meloe augustcollis* Say were reported for the first time in New Brunswick. Also, *E. pestifera* was newly recorded [167].

In U.S.A., fourteen of the Florida species are limited largely or entirely to the Atlantic and/or Gulf coasts. Twelve species are more or less widely distributed in the central and/or eastern states. Two species occur both in the southeastern states. These two species belong to South and Central American groups and probably reached the continental U.S. from the islands. A third, weaker faunal link with the West Indies is represented by *Pseudozonitis longicornis* (Horn), whose group includes one West Indian species and two relictual species in east Texas and no species is indigenous [168, 169]. Molestan blister beetle *Lytta molesta* (Horn] occurs in Central California and adults were often found on flowers and had been collected on *Lupinus*, feeding on its flowers and seed pods [170], on *Trifolium wormskioldii* in dried vernal pools, and on *Eriodium* [171]. In addition, a historical perspective and results of an intensive alfalfa survey blister beetles in Kansas was published [172, 173]. Certain species of *Lytta* in the western U.S. had been identified as ‘species of concern’ by the U.S. Fish and Wildlife Service and *Lytta unguicularis* (LeConte) in the Great Smoky Mountains National Park may represent a similar case [170]. The Hopping's blister beetle *Lytta hoppingi* Wellman was found in the foothills in the southern end of the Central Valley, Kern County and Fresno and Tulare counties; the Morrison's blister beetle *Lytta morrisoni* (Horn) occurs in the southern Central Valley, Fresno County, Carrizo Plains in San Luis Obispo County, Tulare County and Kern and San Benito counties; the Mojave Desert blister beetle *Lytta insperata* (Horn) was known only from "Mojave Desert" (the type locality), San Diego, and Ventura County [170].

The *Tetrastichus incertus* (Ratzeburg) was rediscovered from *Hypera postica* (Gyllenhal] in the Mesilla Valley, New Mexico [174]. Buntin [175] reported the occurrence of some blister beetles in Georgia alfalfa. Pinto [176] recorded a new *Meloe* Linnaeus from southern California chaparral as a rare and endangered blister beetle or simply secretive. Certain species of blister beetles in alfalfa in Kentucky was observed [16]. Some facts about the blister beetles in North Carolina State were mentioned [177]. Sansone and Knutson [178] reported some blister beetles in Texas. The striped blister beetle *E. vittata* is a native species in USA. Some samples of this species were collected from all eastern states west to, and including, South Dakota, Nebraska, Kansas and Oklahoma [166]. The occurrence of *L. unguicularis* on hybrid azaleas in the Great Smoky Mountains National Park (USA), representing the first time in the Park since the late 1950s and early 1960s, was reported [179]. The *Gnathium* spp. are limited to the western and southern United States and northern Mexico [180]. The orange blister beetle *Zonitis* spp. was observed in the Brisbane area, Queensland, Australia [181, 182].

In **Central and South Americas**, certain meloid beetles of the West Indies were recorded [169]. The blister beetle *Cissites auriculata* (Champion) was recorded from the Atlantic slope (San Geronimo) as well as from the Pacific side of the country [183]. For more details, the genus *Cissites* Latreille is represented generally in the New World by two species, *Cissites maculata* (Swederus) and *C. auriculata* [184-186]. Selander and Bauseman [I69] and MacSwain [187] indicated that *C. maculata* is found from North Mexico to Argentina, including the West Indies and the Galapagos Islands, while *C. auriculata* extends from approximately the same northern latitude to Honduras in the south. In Guatemala, it appears that *C. auriculata* is the more abundant [188]. Among the beetle fauna of Lesser Antilles, the blister beetle *C. maculata* (in subfamily Nemognathinae, tribe Horiini) was reported in Barbados, Cuba, Dominica, Guadeloupe, Hispaniola, Puerto Rico, St. Vincent. Argentina, Brazil, Chile, Colombia, Ecuador, French Guiana, Mexico to Panama to Peru, Trinidad and Venezuela [189]. Also, the same blister beetle was reported in Barbados, Cuba, Dominica, Guadeloupe, Hispaniola, Montserrat, Puerto Rico, St. Vincent. Mexico to Panama, Colombia, Ecuador (including Galapagos), Trinidad, Venezuela, French Guiana, to Peru, Argentina, Brazil, Chile [190] and in Galápagos Islands, of Ecuador [191].

The bella species group in the genus *Epicauta* was primarily distributed in the Chaco subregion, ranging from southern Bolivia, western Paraguay, southern Brazil, and central and northern Argentina [192-195]. The blister beetles of the genus *Epicauta* were reported as the most important chewing herbivores in the dry forest of Santa Rosa National Park, Costa Rica [196]. The knowledge on the geographical distribution of each species of the genus *Epicauta*, in South America was updated [197]. Also, two new *Epicauta* from Mexico were studied [198]. The oil beetle *Pyrota rugulipennis* (Champion) was recorded in Central America and the meloid *Pyrota* was found in Mexico [199]. For the genus *Tetraonyx* spp. in Argentina, a synopsis was provided [200]. *Tetraonyx* spp. were recorded from *Epicharis* bee nest in the island of Tobago, Trinidad and West Indies [201]. The *Tetraolytta gerardi* (Pic), as an enigmatic blister beetle from Brazil, was rediscovered [202].

Pseudozonitis marginata (Fabricius) was reported within tribe Nemognathini and distributed in Bahamas (Andros), Cuba, Dominica, Grenada, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, St. Croix, St. Lucia. A list of species of Meloidae that occurs in State of Rio de Janeiro (Brazil) was published [203]. Peck [204] provided a summary of the published diversity of the beetle fauna of St. Lucia, and provided a starting point for future research. The published beetle fauna of the island of St. Lucia was summarized. In the family Meloidae, he reported the blister beetle *P. marginata* belonging to the subfamily Nemognathinae (tribe Nemognathini) and distributing in Bahamas (Andros), Barbados, Cuba, Dominica, Grenada, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Croix, St. Lucia; widespread Antilles endemic. After a year, a summary and analysis of the published records of the beetle fauna of the island of St. Vincent was provided as a contribution to a long term project to understand the diversity, evolution, and distribution of the beetles of the Lesser Antilles [190].

In the book "Beetles of the Galápagos Islands, Ecuador Evolution, Ecology and Diversity", Peck [205] presented the previously published information and abundant new data gathered during extensive recent field studies on Galapagos beetles including 486 species with detailed information on their distribution and bionomics, although the origin and biogeography of the beetles (Coleoptera) of the Galápagos Archipelago was comprehensively studied before [206]. The big-eared blister beetle *C. auriculata* was introduced into Hawaii in 1934 in an attempt to decrease the population of *Xylocopa sonorina,* the bee being sometimes considered a pest because it nests in the wood of buildings [188, 207]. It apparently no longer occurs in Hawaii [207]. Unfortunately, no reports of the meloid distribution in the **Australian** and **Papuan region** [163].

Comprehensive Systematics of Meloidae

The comprehensive classification of the Meloidae was made by Kaszab [208]. After more than two decades, Selander [209] provided a classification improvement. In their valuable work, Bologna and Pinto [27] declared that Beauregard [210] published a splendid monograph of the Old World Meloidae including an exhaustive treatment of the pharmacological, anatomical and biological features of the family. As mentioned by Bologna and Pinto [27], some important 19th-century additions including taxonomic studies of several Palaearctic genera were of Abeille de Perrin [211], Escherich [212-220], Haag-Rutenberg [221, 222], Marseul de [223-226], Prochazka [227], Reiche [228], Reitter [229-239], Semenov [240-246], as well as important 20th-century meloid studies had been carried out by Pic [247-257], Cros [185, 258-307], Soumacov [308, 309], Maran [310-316], Kaszab [34, 45, 94-96, 109, 156-158, 208, 317, 318], Pardo Alcaide [38, 39, 106, 122,

[123, 133, 160, 319-330], Kuzin [331, 332] and Bologna [10, 11, 32, 36, 37, 40, 46, 48, 103, 333-340]. Classifications of the Meloidae to the generic or subgeneric level on a worldwide basis in the 20th century had been published by Wellman [341], Borchmann [342], and Kaszab [96]. None of the three paid much attention to the priority of family-group names, nor in general have the many authors who have dealt with restricted segments of the meloid fauna. Horiales and Cantharidiae were the first family-group names applied to blister beetles, both proposed by Latreille [343]. Aksentjev [344] listed the nominal genus-group taxa in Meloidae and their associated type species.

For some details, Selander [209, 345-347] recognized three subfamilies, 10 tribes, 15 subtribes, 116 genera, and 66 subgenera in the family Meloidae while Bologna [10, 11] recognized four subfamilies only: Eleticinae, Meloinae, Tetraonycinae and Nemognathinae. Eleticinae was considered the most basal subfamily of Meloidae [348, 349] but remained almost unknown until the middle of the last century, and was usually included within the subfamily Meloinae. Selander [345] defined it and demonstrated its phylogenetically basal position. Then, Selander [346] revised the systematics of its tribes and genera. Selander's phylogenetic proposal was not accepted by Kaszab [208], who preferred to maintain an "Eleticoid Meloinae" group, by defining different tribal assemblages of genera and also indicating some taxonomic errors introduced by Selander [346]. Pinto and Bologna [163], Bologna and Pinto [27] and Bologna et al. [349] accepted the subfamily Eleticinae, but adopted an intermediate tribal arrangement between those proposed by Selander and Kaszab. However, Bologna [103] reexamined the nomenclatorial arrangement of the same subfamily. In their comprehensive work about the taxonomy and classification of *Meloe* species, Pinto and Selander [65] declared that the most considerable key to the European and northern African species of *Meloe* was that of Reitter [230] and then of Reitter [237]. Also, some early taxonomic studies on the Central and southern African species were carried out by Peringuey [30] and Schmidt [350]. El-Gharbawy [126] revised genus *Meloe* and constructed a key for seven species in Egypt.

Until 1970, there was no comprehensive work on the Asian species, but several species found in the region had been described by Miwa [351]. Bologna [47], established a new genus *Berberomeloe* in Europe and North Africa. Bologna [47] revised, also, the taxonomy of *Eurymeloe*, as a subgenus of *Meloe* among the European, west Asiatic and Mediterranean species of Meloidae. Bologna et al. [352] revised the genus *Actenodia* Laporte de Castelnau which includes 18 species distributed in the Mediterranean and Saharo-Arabian regions, and in eastern and southern Africa. They described the species *Actenodia carpanetoi* Bologna & Di Giulio from Mozambique with a key to all species in the genus. A checklist of 5 genera and 41 species of Meloidae occurring in Xinjiang (China) was provided [73]. A new species in *Epicauta* was identified from Yunnan [75]. Wang et al. [77] discussed the number of species of meloids and constructed a key to the genera of blister beetles in China. Pan et al. [353] reviewed the mylabrine subgenus *Eumylabris* and provided a key to the five Chinese species. In the Iberian Peninsula, a study of the type material of *Zonabris rosinae* Escherich and *Zonabris pauper* Escherich, allowed García-París and Ruiz [154] to confirm the taxonomic criteria for the recognition of these two species established by Pardo Alcaide [319,320]. García-París et al. [354] presented an up to date synonymic list of the Iberian and Balearic fauna of Meloidae including all synonymies for 65 taxa at the species level. For Sardinia, an annotated checklist of Meloidae was presented by Montalto and Bologna [355]. In Poland, keys for the genera and species of Meloidae together with a checklist of species included in the genera *Epicauta, Malybris, Lytta, Alosimus, Oenas, Lydus, Cerocoma, Meloe, Apalus, Stenoria, Sitaris, Zonitis, Stenodera* and *Euzenitis* were provided [128].

Pinto and Selander [65] presented, also, the most important taxonomic works dealing with *Meloe* in the New World such as the LeConte's [356] treatment with the species of the United States, Champion's [183] review of the Mexican and Central American species, and VanDyke's [357] revision of species of North America north of Mexico. Several decades ago, the genus *Meloe* has been segregated from other genera of Meloidae in either a separate subfamily [358] or tribe [345]. Forty nine New World genera of blister beetles were reviewed, a key to the genera was constructed, and a brief synopsis of each genus was prepared [359].

Several works on the meloid taxa, particularly USA, had been published [360-363]. In Central America, the meloid *Pyrota* in the Pacifica and *Nobilis* groups of Mexico were studied [199]. In Mexico, the Meloidae fauna currently includes 255 extant species, plus one only known from the fossil record. A comprehensive catalogue recorded the occurrence of 160 species, almost 100 species less than the current known number [364]. An inclusive taxonomic catalogue of the Mexican representatives of Meloidae was published [365]. In Brazil, *Acrolytta neivai* Denier was returned to *Lytta* as *Lytta neivai*

Denier by Selander [366]. He transferred, also, *Acrolytta nigropicta* Denier from Argentina to *Picnoscus* and *Acrolytta weyrauchi* Kaszab from Peru to *Spastomeloe*. Meloidae from Cuba were revised by Genaro [367]. However, more information on meloid beetles from Cuba were presented in a checklist [368].

Systematics based on adult morphology

Generally, adults of meloid beetles are soft bodied and generally elongate (10-20 mm) with pronotum usually narrower than the base of elytra (fore-wings). 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 is soft with 6 visible sterna. Male genitalia include elongate aedeagus with 1-2 distal dorsal hooks and 1 ventral endophallic hook. Parameres is fused at base only. Phallobase is large. Female genitalia are short and lack long membranous tube-like ovipositor [9].

Diagnosis of genus *Meloe*, as for example, in the adult stage on a worldwide basis is difficult. However, the adult *Meloe* of only the North American fauna are easily recognized by their abbreviated, basally imbricated elytra and lack of hind wings [65]. In all other flightless North American Meloidae, such as *Epicauta conferta* (Say), *Lytta sublaevis* (Horn) and several species of *Eupromphina*, the elytera meet along the sutural (median) margin basally, without overlapping. This elytral character is inadequate for the recognition of *Meloe* in the Old World because imbricate elytra occur also in the lyttine genus *Trichomeloe* [65]. The presence of mesothoracic glands in *Epicauta segmenta* Say and other blister beetles was observed [369]. Fine morphology of antennal and mouth-part sensilla of the blister beetle *Meloe campanicollis* Pinto & Selander was described [370].

In connection with the mouth parts, the adults in subfamilies, Eleticinae, Meloinae, Tetraonycinae and Nemognathinae, except some taxa in which the adults do not feed, are phytophagous and possess prognathous biting-chewing type [163]. In the Nemognathini, species of the genera *Leptopalpus, Nemognatha, Gnathium, Zonitodema, Zonitolytta* and *Zonitis* possess elongated mouth parts which are modified [371] to take up nectar from deep flowers with concealed nectaries [372] as the main food source [318, 373, 374]. Different parts of the maxillae compose the proboscis in Meloidae which is either formed by the elongated four-segmented maxillary palps (*Leptopalpus*: [375]) or by the elongated galeae (*Zonitis*, *Nemognatha* and *Gnathium*: [180, 373]). Although the elongation of mouth parts in Meloidae has been known since the study of Handschin [375], and despite the fact that they are depicted in entomological textbooks as an example of amazing adaptations in Coleoptera [376], detailed studies of proboscis morphology in nectar-feeding meloid species are not reported in the available literature.

We have compiled here some of the almost recently reported systematic works on the **Asiatic genera and species**, basing on the adult morphology. Some contributions were taken place in India [90, 378, 379]. Collected adults of the black blister beetle *M. proscarabaeus* and violet oil beetle *M. violaceus* from the Himalayan region were used for developing a key to the Indian species of *Meloe* [91]. From the Indian subcontinent, Anand [380] studied the male genitalia of 27 species which represent 7 genera including *Mylabris* of the subfamily Meloinae in order to discuss their taxonomic significance. In addition, Mohamedsaid [28] studied the taxonomy of Meloidae in Sri Lanka and constructed keys to 15 species in 7 genera. Some meloid genera and species were classified in Central Asia [63], Saudi Arabia [50], Malaysia [28] and Tadzhikistan [57], depending on the adult morphological characters. In Arabia, also, Kaszab [50] published a synopsis of the Meloidae (in "Insects of Saudi Arabia") and then thirty-three species and subspecies of Meloidae were studied from the Peninsula [381].

A key to the Iranian species of *Mylabris* was constructed [382]. An additional new species, *Mylabris minae* Makhan & Ezzatpanah, was morphologically described from Mahallat, Markazi Province. It appears to be most closely allied to *Mylabris aschnae* Makhan & Ezzatpanah, but it was easily separated by the setae of the tarsus and by the shape of the male aedeagus [383]. The blister beetle *Hycleus golnaze* Makhan & Ezzatpanah was described from Mahallat, Markazi Province, as the second known species of the genus [384]. The blister beetle *H. golnaze* appears to be most closely allied to *Hycleus pierrei* from Iran, but there is a difference in the shape of the male gonoforceps [95].

The taxonomy of the genus *Hycleus* Latreille from China, with description of new species, was given [76]. Also, taxonomic notes on species of blister beetles from Hebei Province were provided [385].

Eleven representative species of *Mylabris* Fabricius from China were analyzed and their hind wings were compared and described by taking *M. calida* as the model. As a result, the venations of *Mylabris* Fabricius were tentatively classified into three types. The hind-wing morphology of *Mylabris* was studied and the vein morphological evolution of the genus was discussed [386]**.** Also, the morphological structures of *Mylabris posticalis* (Dokhtouroff) and *M. calida*, *Mylabris crocata* (Pallas), *Mylabris magnoguttata magnoguttata* (Heyden) and *M. posticalis* were illustrated [77]. More recently, the morphological and anatomical structures of Nemognathini (Meloidae) had been described and new insights were paid to the functional aspects of proboscis in nectar-feeding Meloidae [387].

In Taiwan, Meloidae is a small family which is composed of 11 known species, and having parasitic relationship with grasshoppers of Orthoptera or social wasps of Hymenoptera. *Meloe* is the only genus without hind wings. A good example, *Meloe formosensis* Miwa, was morphologically described [388]. Different *Epicauta* spp., namely *Epicauta horaki* Dvorak sp. nov. (from Vietnam), *Epicauta promerotricha* Dvorák sp. nov. (from Uttar Pradesh, India), *Epicauta probsti* Dvorák sp. nov. (from Nepal), *E. dalihodi* sp. nov. (from Taiwan), *Epicauta thailandica* Dvorák sp. nov. (from Thailand] and *Epicauta schneideri* Dvorak sp. nov. (from Thailand) were described. Also, new faunistic data of *Epicauta cheni* Tan and *E. curvispina*, from Vietnam, were presented [389]. Bologna and Nikitsky [390] described and figured *Lytta zubovi* Bologna sp. nov., a new species of Meloidae from Crimea (Ukraine).

In regard to systematics of **African genera and species**, a new species of *Meloe*, *M. rugosus*, related to species of *M. murinus*, was described in northwestern Morocco [391]. In his very valuable monograph on Coleoptera of Egypt, Alfieri [44] classified the family Meloidae, on the basis of morphological characters, into two subfamilies, Lyttinae and Nemognathinae. Lyttinae includes three tribes (Mylabrini, Lyttini and Meloini) and Nemognathinae includes three tribes (Sitarini, Nemognathini and Horiini). In the steppe area of Tlemcen (Algeria), a biometrical study of two species of *Mylabris*: *M. oleae* and *M. calida* was carried out [392]. Descriptions of meloid beetles were included in the descriptive catalogue of the Coleoptera of South Africa [30]. The genus *Iselma* is strictly distributed in the western portion of Southern Africa. Some taxonomic misinterpretations and described nine new species in the genus were clarified [393]. In their valuable work, Bologna et al. [352] described briefly and illustrated the adult morphology of 18 species in the genus *Actenodia* which distributed in the in eastern and southern Africa in addition to Mediterranean and Saharo-Arabian regions. Information on the colour variability of *Meloe csikii* Kaszab from Kenya was given beside a new key to the genera of the tribe Morphozonitini [113]. On the basis of morphological analysis, the same genus was investigated and the endemic diversification of the Cape zone (South Africa) fauna with the phylogenetic relationships among the 30 species was clarified [112].

Several works had been published for the **European genera and species**. In Turkey, 56 species in 12 genera of Meloidae were recorded and two species, (formerly known as *Mylabris zebraea* Marseul and *Mylabris scabiosae* Olivier), were transferred to *Coryna* [46]. The blister beetle *T. kulzeri* was described from "Arm. Taurus, Moks" [317] as well as many new species from various localities were described and classified [45]. Diagnostic features of the specimens collected from Bitlis conform to the re-description prepared by Bologna and Di Guilio [394], especially apically expanded last abdominal tergite of the males. Recently, Kocak and Kemal [395] studied 178 species of Meloidae from Turkey giving them synonymous names.

Many faunistic and taxonomic publications for the meloid genera and species in the Iberian Peninsula, based on morphological characters, are available in the literature. The Meloidae include records from authors of the 19th and early 20th centuries, but in most cases the main reference was to that of Górriz and Muñoz [52]. In the present century García-París and Ruiz [396] published a comprehensive work, containing the Iberian records of earlier Meloid species. They discussed the different possibilities for species description when the original nomenclature did not correspond with that presently used. With regard to the blister beetle *Stenoria antoinei* Pardo Alcaide in the Iberia, the main diagnostic traits were exposed, especially those related to the aedeagus. Also, distinctive traits among the Iberian species of genus *Stenoria* Mulsant (*Stenoria apicalis* Latreille*, S. antoinei* and *S. analis* Schaum) were presented in a diagnostic key [397]. The current taxonomy of the genus *Euzonitis* is mostly based on elytral and pronotal pilosity, integument sculpture and coloration; a set of characters that show a relatively high degree of intraspecific variation in blister beetles [10, 11]. In the south of Iberia, the blister beetles *Z. fernancastroi* and *Z. flava* Fabricius had been discriminated basing on the morphological traits with special emphasis on the characters provided by the aedeagus [152]. The blister beetle

Mylabris deferreri Ruiz & García-París was morphologically described and differentiated as a new species from the mountains of southeastern region of the Iberia (Granada, Spain). Also, the species *Euzonitis haroldi* Heyden was almost unknown taxon, sometimes treated as a variety of *Euzonitis quadrimaculata* (Pallas), originally described from Central Spain and only known from a few localities in Spain and Morocco [398]. Alcobendas et al. [399] analyzed and compared morphological (and molecular data] of the two taxa concluding that *E. haroldi* is genetically and morphologically identical (except for coloration) to *E. quadrimaculata*, and therefore *E. haroldi* should be treated as a junior synonym of *E. quadrimaculata* (syn. nov.). However, additional information on the morphological characters of adult meloids of Old World taxa are available [25, 108, 394, 400- 418].

Special attention should be paid to the meloid **American genera and species**. The genus *Meloe* is primarily a continental and montane genus in North America. The blister beetle *Meloe ajax* Pinto, as a new species of *Meloe* Linnaeus in the subgenus *Treiodous* Dugès was described from southern California chaparral [176]. In both Central and South Americas, different species of the family Meloidae had been classified in the subfamily Eleticinae which consists of tribes Spasticini, Lyttini, Pyrotini, and Epicautini. The subfamily Tetraonycinae includes tribe Tetraonycini, as well as subfamily Nemognathinae includes tribe Nemognathini. For more details, several species of the tribe Lyttini in the subfamily Meloinae in Argentina were identified [364]. Bologna and Pinto [202] redescribed the blister beetle *Tetraolytta gerardi* (Pic), in the monotypic genus *Tetraolytta* Pic which is endemic to southern Brazil, and discussed its position relative to the other genera of Tetraonycinae. New South American species group of the genus *Epicauta* was redescribed and illustrated, including both external morphology and female and male genitalia, for the first time [197]. However, the literature contains some other taxonomic works on Meloidae, based on the morphologically diagnostic characters [419-450].

Systematics based on larval morphology

The majority of morphological studies on the meloid beetles focused on the first or first and second larval instars (triungulins) and other immature stages as important tools or measures to disclose the taxonomic problems among taxa of this family. The presence of triungulins is the most interesting aspect of the life history of most taxa of blister beetles. The triungulin first instar, depending on the group, seeks out a food source consisting of eggs of Acridoidea (Orthoptera), or provisions and larvae of Apoidea or other aculeate Hymenoptera [10, 11, 348]. The phenomenon of phoresy has historically been given considerable weight in the classification of Meloidae because the phoretic triungulins have several common structural features [451] such as the well sclerotized body correlated with a prolonged exposed existence before encountering food, and modifications of the head and legs adapted for grasping the setae of its host [65, 451].

On the basis of larval morphology of the first instar, MacSwain [358] reviewed the family Meloidae and summarized the triungulin structure in four subfamilies (Tetraonycinae, Horiinae, Nemognathinae and Meloinae) which were collapsed later in two, Nemognathinae and Meloinae [345]. The triungulin description was used as a tool for systematics of *vittata* group of the genus *Epicauta* [452].

The genera and subgenera of the tribe Meloini were discussed and a new key for their classification was proposed depending on the triungulin structure [453]. The first instar larva of *M.* (*Taphromeloe*) *erythrocnemus* was described and compared to larvae of other species of the genus [454]. The triungulin description was used as a tool for systematics of *L. dusaulti* [400]. The first instar larvae of *Meloe* (*Treiodous*) *afer* Bland, and *Meloe occultus* Pinto & Selander were described and compared with other members of their subgenus. Antennal segment II and its associated sensory organ were important in the systematic of the genus *Meloe* [415]. The triungulin description was used as a tool for systematics of *Synhoria testacea* (Fabricius) [408]. Yanega [455] reported the beetles associated with bee nests (Hymenoptera: Apidae) in Chiapas (Mexico) and described the immature stages of *Vanonus balteatus* Werner. The first instar larvae of *Meloe* (*Lasiomeloe*) *olivieri* Chevrolat and *Meloe* (*Micromeloe*) *decorus* Brandt & Erichson were described and a comparative analysis of morphological characters of these taxa with other subgenera was provided [403].

In the present century, some observations of triungulin larvae of *M. proscarabaeus* Linnaeus in the warm spring of 2000 had been given [129]. Bologna et al. [456] reviewed the primitive blister beetle genus *Iselma*, of South Africa, depending on the triungulin description. The triungulin description was used as a tool for systematics of *M. variegates* [457], *Cyaneolytta* [413], the Neotropical genus *Epispasta* [414], the genus *Diaphorocera* [416], the subtribe Lydina [417], and the genus *Berberomeloe* [418]. The

Southern African genus *Prolytta* Kaszab was reviewed on the basis of first instar larva description [405]. The genus *Stenodera* was reviewed with a description of first instar larva of *Stenodera puncticollis* [444]. A larval morphology of the genus *Cerocoma* was provided [412]. Bologna and Di Giulio [406] morphologically described the eggs and first instar larvae of *Prionotolytta binotata* (Péringuey) as an endemic southern African species. The first instar larval morphology was described for *Euzonitis rubida* (Menetries) from the Iberian peninsula [25] and be confirmed its closeness to *Zonitis* Fabricius as previously suggested by Bologna [10, 11]. The first description of the triungulins of *M.* (*Meloegonius*) *rufiventris*, *M.* (*Micromeloe*) *uralensis* and *M.* (*Eurymeloe*) *scabriusculus* was illustrated beside the discussion of systematic relationship to closely related species. A key to identify all triungulins of the genus *Meloe* from Central Europe was given [458]. The first instar larvae of two species, *Actenodia chrysomelina* (Erichson) from southern Africa and *Actenodia denticulata* (Marseul) from Arabia, were described for the first time and compared with two other Palaearctic species described previously [352]. Di Giulio et al. [410] prepared the first comparative morphology of first instar larvae of Meloidae from Australia. They described the first-instar larva of one species of the endemic genus *Palaestra*, as well as those of other phoretic species without adult association and consequently unplaced to genus.

It is worth mentioning some morpho-ethological studies reevaluated the value of phoretic habits in the Meloinae tribes [348], and few molecular phylogenetic studies [349] defined in a new way the relationships of several genera and tribes. The molecular studies, however, will be discussed in the present review.

Systematics based on Internal Anatomy:

As shown in the available literature, some authors studied the anatomical structures aiming to disclose certain taxonomic problems in the family Meloidae, while other did not intend so. Although the Meloidae provides an excellent source of material for anatomical and morphological study, some of the early taxonomic works on the different genera included discussions of external morphology as it related to classification [459]. Unfortunately, the literature contains no recent works. Considering the musculature, skeletal musculature in larval phases of the beetle *E. segmenta* was described [460]. The head musculature in the adult *L. vesicatoria* [461] and *E. segmenta* [462] was described. The latter author compared the head musculature of adult with those of immature stages observing considerable differences in maxillary musculature. A discussion of the correspondence in musculature between *E. segmenta* and other known Meloidae was also provided [462].

Several internal organs and systems had been investigated but the most attractive to research are the digestive, reproductive, nervous, and excretory. At an earlier time, Everly [463] described the alimentary tract of the margined blister beetle, *Epicauta cinerea marginata* Fabricius collected in Southern Ohio (USA). In his work, the morphology and histology of fore, mid- and hind-guts were dissected and illustrated. Almost two years later, a similar study was conducted for the black blister beetle, *Epicauta pennsylvanica* (De Geer) [464]. The digestive systems of 46 meloid species, representing 32 genera from North America, Europe, North Africa, and India, were studied, and a subfamily and tribal system based on these internal systems was proposed [465]. Depending on the study of digestive systems of 5 North African blister beetle species, the genera *Rusadiria*, *Lagorina* and *Sitaris* were assigned to the tribes Mylabrini, Lyttini and Nemognathini [466]. On the basis of digestive structures of the South American blister beetle *Picnoseus nitidipennis* (Fairmaire & Germain), its genus had been tentatively placed in the tribe Lyttini [467]. On a random collection of the Clematis blister beetle, *Epicauta cinerea* (Forster], lesions in various regions of the mid-gut were observed and histologically described [468].

The mesothoracic glands in the blister beetle *Mylabris pustulata* (Thunberg) [469] the blister beetles *L. nuttalli* and *Lytta viridana* Le Conte [470] were studied. Thereafter, Berrios-Ortiz[369] described the mesothoracic glands of the blister beetle *E. segmenta* and found no significant differences between glands in males and females in regards to structure and form. Depending on the results of latter study, also, females of 41 other species in genus *Epicauta* were checked for the presence of glands, 37 of which showed glands, 2 species showed orifices but no glands, and 2 species showed no evidence of either. It was concluded that the occurrence of mesothoracic glands, peculiar to the Meloidae is a generalized character.

In connection with the reproductive system in Meloidae, 46 meloid species, representing 32 genera from North America, Europe, North Africa, and India, were revised on the basis of their reproductive organs, and a subfamily and tribal system was proposed [465]. Gupta [466] studied the reproductive

systems of the representative species of the genera *Rusadiria*, *Oenas, Lagorina*, *Sitaris* and *Zonitis* from North Africa. Also, the reproductive system of *P. nitidipennis* from South America was described [467] and a systematic study of the blister beetle *Pseudomeloe miniaceomaculata* (Blanchard) was carried out [471]. On the basis of these internal anatomical features, such as the absence of a basal spermathecal diverticulum, a tubular female accessory gland, an irregularly convoluted first pair and a recurved or bent second pair of male accessory glands, this genus was placed in the tribe Eupomphini of the subfamily Meloinae. The inclusion of *Pseudomeloe* in Eupomphini now extends the distribution of this tribe to South America as well. Also, the structure, formation, histochemistry, fate and function of the spermatophores of *L. nuttalli* had been studied [472]. Using the adult males of another blister beetle, *M. indica* (Thunberg), morphological and histological characteristics of the reproductive organs were examined [473].

On the other hand, the external and/or internal genitalia have obtained more interest of research in different parts of the world and may be used as a systematic measure for the family Meloidae. Herein, it may be important to refer to some reported works. The external genitalia and their musculature in both sexes of the desert blister beetle, *L. vulnerata* were identified, illustrated and discussed [466]. Gupta [474, 475] provided a significance of the external genitalia on the higher classification of Meloidae. The anatomy and histology of the male and female internal genitalia of *L. nuttalli* Say and the various organs during copulation and oviposition were described [476]. Afterwards, the external genitalia of the same meloid species had been studied [477]. On the basis of external genitalia, Gupta [478] provided a significance of some genitalic components in the higher classification of the family Meloidae. Also, the taxonomic significance of the male genital apparatus of 27 species representing 7 genera of the subfamily Meloinae from Indian subcontinent was mentioned [380]. The male genitalia of 20 species of Meloidae from Xinjiang Uygur Automous region were comparatively studied [479]. In view of results of the latter study, it was concluded that characteristics of the male genitalia, like other external characters, can be used in the identification and classification of the species.

In addition, a few works had been carried out for other internal organs, such as the malpighian tubules of the orange blister beetle, *M. pustulata* [480], the cephalic neuroendocrine systems of the same beetle [481], and the exocrine glands in the mesothorax of *L nuttalli* Say [470].

Systematics based on sexual behaviour of adult beetles

The study of sexual behaviour has been largely utilized in phylogenetic analyses of meloid beetles. Although the sexual and egg laying behaviour characters represent helpful tools for the Meloidae classification, the available literature does not contain recently published articles. However, some of the published research works are reviewed herein. As reported in an evolutionary discussion, Nemognathinae and, by inference, Eleticinae have simple courtship behavior but Meloinae have more elaborate courtship. Moreover, the courtship behavior in *Pyrota* is both complex and highly distinctive [345]. A taxonomic revision of the genus *Megetra* with ecological and behavioral notes was provided [482]. Male courtship behavior in *Linsleya convexa* (LeConte] was described in detail and patterns of courtship in this species and other Meloinae were compared briefly [483]. Behavioral patterns associated with egg-laying were proposed as a potentially valuable source of taxonomic characters for blister beetles that excavate oviposition chambers in the soil. Relationships among species of *Lytta, Linsleya*, and *Epicauta*, suggested by their nesting behavior, were compared with those indicated by other characteristics [484]. Comparative courtship behaviour of *Negalius, Phodagaand, Cordylospasta*, three closely related genera of blister beetles, was described [485]. The pattern of courtship in *P. alticeps* was compared to that of other meloids. Particular attention was given to the behavior in its closest relative, *Negalius marmoratus* Casey [486]. The courtship and copulation in the blister beetle *Lytta nuttalli* Say was studied. Abdominal vibration seems to be unique to *Lytta*, whereas the dorsal orientation during courtship and the genital activity are similar to those observed in many other Meloinae [487].

On the basis of courtship behavior, Pinto [488] revised the taxonomy of three North American species of spotted *Epicauta* which are found to be a heterogeneous group of blister beetles. He provided keys for separating *E. bispinosa* Werner*, Epicauta punctipennis* Werner and *Epicauta cazieri* Dillon from one another and from the Maculata Group. In the same year, a published paper contained the description of courtship behavior in the 3 allopatric species of *Tegrodera* and concluded its distinction from that of all other meloids. Courtship in this genus was most similar to that in Eupompha and Pleurospasta. Yet because of certain differences in behavior and associated structure, these

similarities were attributed to convergence [489]. Concerning another meloid genus *Cysteodemus*, the description of sexual behaviour in two species indicated that those behavior represents a condition intermediate between that found in the Meloinae and Nemognathinae, the two major subfamilies of blister beetles [490]. Pinto [491] expanded the study to compare the sexual behaviour in 18 species, representing all 8 genera of the subtribe Eupomphina and described the behavior in *Cordylospasta fulleri* Horn*, Pleuropasta mirabilis* (Horn)*, Eupompha viridis* (Horn), *Eupompha edmundsi* (Selander), *Eupompha schwarzi* Wellman*, Eupompha histrionica* (Horn), and *Eupompha fissiceps* (LeConte) for the first time. He concluded that courtship behavior patterns is probably of little value for higher classification but its greatest potential is at the species level.

Field collections of three species of Meloidae, *Lytta vulnerata* (LeConte) and *Epicauta ochrea* (LeConte) and *Tegrodera erosa* LeConte were obtained. The first two species mated assortatively for size but the third species did not. A discussion of possible selective advantages of unmounted versus mounted display in the Meloidae was included [492]. The courtship and other behavior patterns were described in adults of the Ethiopian blister beetles *Cyaneolytta fryi* (Wollaston) and *Cyaneolytta maculifrons* (Maklin). On the basis of behavioral characters, and anatomical characters of the triungulin larva, *Cyaneolytta* was transferred from the tribe Lyttini to the tribe Meloini [366]. Considering the courtship behaviour for several species among 173 North American blister beetles of the genus *Epicauta*, the treatment of these species was conducted taxonomically. Two subgenera were recognized: the nominate subgenus with 101 species, and Macrobasis with 72. Among taxonomic changes were 6 new species and 10 new synonymies [165]. Early in the present century, the sexual and cleaning behaviour of the blister beetle *Lydus trimaculatus* Fabricius was described and information on courtship of other six species of different genera of the tribe Lyttini, observed in the field, was also given. Comparative analysis of the courtship, both from literature and field records, of eight genera was achieved [493]. The courtship behavior of *M.* (*M.*) *decorus* and *Sitaris muralis* (Foerster) was described by Lückmann [494]. He showed, also, the differences to other subgenera within the genus *Meloe*. However, additional information about the sexual behaviour as a helpful measure for the systematics of Meloidae can be obtained from literature [65, 171, 487, 495-504].

Systematics based on phoresy of triungulins

Phoresy is the act of one organism attaching to another for the purpose of dispersal. In Meloidae, the beetle triungulins (first instar larvae) attach themselves to the hairs of the host bee body in order to be transported to the bee nest in which they feed on eggs and provision. Phoresy behaviour may be useful for the Meloidae systematics. [456,501]. In his review of the family, MacSwain [358] stressed on the triungulin structure, and summarized its presence in four subfamilies, Tetraonycinae, Horiinae, Nemognathinae and Meloinae. Phoresy, characterizing all four, was the only justification for separating Meloinae from a fifth subfamily, Lyttinae. As defined by MacSwain and certain earlier authors [505], Meloinae was restricted to the Holarctic genus *Meloe* Linnaeus. Unlike the distinctive adults of the other phoretic taxa, those of *Meloe* do not differ significantly from those of numerous genera placed in Lyttinae. Selander [345] collapsed MacSwain's five subfamilies into two, Nemognathinae and Meloinae, the latter including *Meloe* and numerous non-phoretic taxa. Although no longer according *Meloe* subfamily status, Selander continued to emphasize phoresy by placing the genus in its own tribe, Meloini [348].

Systematics of Meloidae based on Molecular Data

Taxonomy is suffering from an important lack of funding. Funding for taxonomy is inadequate and largely diverted to studies of phylogeny, while thousands of species are threatened by imminent extinction [506]. In fact, many authors think that development of theoretical and technological advances in phylogeny reconstruction, in combination with advances in molecular biology, have both driven and consumed much of systematic biology in detriment to traditional taxonomy [507]. As a means to revitalize traditional taxonomy and help it rise above the taxonomic crisis, alternative and complementary approaches have been promoted, for example; molecular taxonomy [508, 509], information technology, the development of investment funds [510] and increased utilization of cybertools [511]. Among those proposals, DNA barcoding [509] has been particularly successful in the identification and delimitation of new species from various groups [512-515]. This method has received increased acceptance because it is simple and affordable [516]. In spite of the wide acceptance of DNA-based methods, however, a large portion of the taxonomic community has rejected them,

fearing that they will deviate funds and incentives from, and represent a threat to traditional morphology [517- 519].

Evaluation of the available literature shows that most of the cytogenetic and molecular biology researches on the family Meloidae had been conducted for disclosing some elusory systematic problems. Chromosomes and phylogeny of the family was studied [520] and a list was presented [521] containing data on chromosome numbers and sex determining mechanisms of 90 species of Argentina beetles, belonging to the coleopterous families amongst which was Meloidae being represented by 3 species. The mitotic and meiotic chromosomes of the beetles *Epicauta atomaria* Germar (Meloidae) and *Palembus dermestoides* (Tenebrionidae) were analyzed. Also, Shao and Huang [522] carried out some Karyotypic studies on six species of Meloidae in Xinjiang (China). A general study on holometabolous insect phylogeny, based on the nuclear 18S and 28S ribosomal RNA (rRNA) genes, was conducted [523]. In this study one species of *Meloe* Linnaeus (*M. proscarabaeus* Linnaeus) was thoroughly examined. In the present century, mitotic and meiotic chromosomes of the blister beetle *E. atomaria* was analyzed in a study which described also on the diploid and haploid chromosome numbers, the sex determination system, the chromosomal morphology, the C-banding pattern and the chromosome(s] bearing NORs (nucleolar organizer regions) [524]. The first report about the occurrence of recombination nodules (RNs) in spread pachytene cells of the blister beetle *E. atomaria* was provided by Zacaro et al. [525]. As pointed out by these authors, the blister beetle *E. atomaria* has 2n = 20 chromosomes including an Xy (p) sex determination system. After a phylogenetic study of Meloidae, based on morpho-biological characters of larvae and adults [348], Bologna et al. [349] studied the family Meloidae on the basis of the molecular characteristics (mtDNA 16S, nDNA ITS2). New molecular research was in progress on the tribe Lyttini to clarify its monophyly and the relationships among genera, and new taxa have to be described [390]. In addition, the relationships among genera of the tribe Mylabrini were clarified using 16S mitochondrial DNA (mtDNA) sequences [526]. Comparison of the molecular data on two taxa of genus *Epicauta* was analyzed [399]. Depending on the results of the latter study, the blister beetle *E. haroldi* was genetically (and morphologically) identical, except for coloration, to *Epicauta quadrimaculata* (Fabricius), and therefore *E. haroldi* should be treated as a junior synonym of *E. quadrimaculata* (syn. nov.).

Recently, the genus *Iselma* was investigated basing on the molecular (mtDNA 16S) analysis in the Cape zone (South Africa) [112]. Molecular studies on the tribe Lyttini resulted in the incorporation of some genera in this tribe, such as *Cyaneolytta* and *Spastonyx* Selander, which had been previously referred to Epicautini or Meloini, respectively [13]. As discussed, Eleticinae are the basal group of Meloidae, according to both morphological (adult and larvae) and molecular evidences [456, 501].

In **conclusion**, different genera and species of the family Meloidae (true blister beetles) are widely distributed in the world. These beetles inhabit various temperate and arid regions as well as sub-tropical and tropical savannas. The literature contains a plenty of reported works on the distribution of meloid beetles in Old World and New World but the reported works on Australian and Papuan meloids are very scarcely. In the field of meloid classification, systematists are considerably interested in the morphology of immature and adult stages and less in the internal anatomy and behavioural characteristics. The least, but more advanced, trend of meloid systematics is obviously the molecular analysis technologies. The latter approach should be widely adopted in order to disclose some elusory systematic problems in the family.

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