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Evolution and biogeography of flea beetles (Coleoptera: Chrysomelidae: Galerucinae: Alticini)

Evoluce a biogeografie dřepčíků (Coleoptera: Chrysomelidae: Galerucinae: Alticini)

Bachelor’s Thesis

Supervisor: Mgr. Martin Fikáček, Ph. D.

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval/a samostatně a že jsem uvedl/a všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, dne 4. 5. 2017

Albert Damaška

Poděkování

Tato práce je výsledkem mé dlouhé, složité a zajímavé formace směrem k biologické práci, která by se vůbec neobešla bez vlivu, pomoci a přátelství řady skvělých lidí. Na prvním místě zde děkuji svým rodičům, že mě dali svobodu zvolit si studium entomologie, všeobecně mě podporovali a v neposlední řadě mě také v roce 2006 poprvé umožnili zakusit nádheru a rozmanitost tropického lesa. Děkuji svému školiteli Martinu Fikáčkovi za trpělivost hodnou světce, velikou podporu a skvělé zázemí, a za spoustu inspirativních nápadů k další práci. Dík patří i ostatním kolegům z Entomologického oddělení Národního muzea. Kolegovi Alexanderu Konstantinovovi děkuji za spolupráci a konzultaci při společném výzkumu mechových dřepčíků. Kolegovi Janu Bezděkovi děkuji za pomoc v nalezení článků, které chybí i v knihovně Národního muzea. V neposlední řadě děkuji také všem, kteří stojí za webovou aplikací Sci-hub, neboť jejich služba vědě je nedocenitelná. Dále děkuji těm, kteří mi poskytli zázemí, vědomosti a podporu v dětství, kdy se mé nadšení pro entomologii objevilo, především Pavlu Špryňarovi, Jaromíru Strejčkovi a Janě Dobrorukové. Velký dík patří i všem mým přátelům a kolegům, kteří mi umožnili již na gymnáziu vstoupit do společenství naší fakulty skrze Biologický kroužek pro středoškoláky, Arachne a především Fluorescenční noc, a také všem kolegům z naší fakulty, že jsem díky nim mohl objevit svět moderního vědeckého výzkumu, a že vydrželi mou přítomnost i v době, kdy vydržet nešla. A především děkuji těm, kteří mi byli a jsou přáteli, protože bez takových se těžko dýchá, hlavně Míšovi Mikátovi, Kátě Jůzové, Anně Koukolíkové, Majdě Holcové, Lukáši Sekerkovi, Tomáši Smyčkovi, Jirkovi Hadravovi, Petru Šímovi, Danu Bendovi, Lukáši „Zbojníkovi“ Janošíkovi, Evče Matouškové, Celii Korittové, Honzovi Pražákovi, Vítu Burešovi, Radku Krisovi Lučanovi, Doubravce Požárové a ještě mnoha dalším. Nejvíce pak děkuji Bohu, za nás a za celý svět, a za všechny ty fascinující organismy, které můžeme studovat. Svůj dík vyjadřuji slovy Žalmu 104, která ke stejnému účelu použil již v roce 1758 C. Linnaeus v preambuli desátého vydání Systému přírody.

Jak nesčetná jsou tvá díla, Hospodine! Všechno jsi učinil moudře; země je plná tvých tvorů.

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O LORD, what a variety of things you have made! In wisdom you have made them all. The earth is full of your creatures.

Abstrakt

Mandelinkovití brouci patří k nejdiverzifikovanějším skupinám hmyzu a v rámci této čeledi se nejvíce popsaných druhů řadí mezi dřepčíky. Tato práce shrnuje dosavadní znalosti o jejich příbuzenských vazbách k ostatním skupinám mandelinek (především bázlivcům) a srovnává různé názory na jejich fylogenetickou pozici, a vnitřní systematiku. V práci též shrnuji známé fosilní nálezy dřepčíků a diskutuji jejich systematické postavení a evoluční, jakož i biogeografický význam. Za svůj úspěch dřepčíci pravděpodobně vděčí i řadě unikátních znaků, jako je například schopnost skákat, a také překvapivě široké škále ekologických přizpůsobení, kterých mohou nabývat. V práci diskutuji jak morfologická, tak i ekologická specifika dřepčíků a speciální důraz kladu na zdánlivě okrajové životní strategie dřepčíků – život v půdní hrabance a v mechu, neboť právě v těchto ekologických nikách se v poslední době ukazuje být rozsáhlá a nepopsaná diverzita dřepčíků. Mechoví dřepčíci jsou navíc, vzhledem ke sníženým disperzním schopnostem a častému endemismu, zajímavou modelovou skupinou pro ekologicko-evoluční a biogeografické studie. V práci také diskutuji současné rozšíření dřepčíků a zabývám se otázkami po vzniku a dynamice jejich areálů. Předkládám také teorie o možných mechanismech disperze nelétavých dřepčíků.

Klíčová slova

Chrysomelidae, Galerucinae, Alticini, biogeografie, fosílie brouků, taxonomie, fylogeneze, disperze hmyzu

Abstract

Leaf beetles belong to most diverse groups of insects and the biggest diversity inside this group is among flea beetles. This work summarizes existing hypotheses about their relationships with other groups of leaf beetles (especially galerucines) and compares various hypotheses about their phylogenetic position and suprageneric systematics. I also rewiev known fossils of flea beeltes and discuss their systematic position and evolutionary or biogeographic significance. The success of flea beetles is likely caused among others by their specific characters, (e. g. their jumping ability), and also their ability to reach dozens of various strategies and ecological adaptations. I discuss both morphological and ecological specifics of flea beetles and especially, I focus on apparently marginal life strategies – terrestrial and moss inhabitance, because in these ecological niches, an interestingly big diversity of flea beetles is uncovered recently. Moss-inhabiting flea beetles are also a very interesting model for ecological, evolutionary and biogeographical studies, because of their high endemism and low dispersal abilities. I also discuss extant distribution of flea beetles in the work and I concern questions about the origins and dynamics of their distributional ranges. I propose theories on possible dispersal mechanisms of non-volant flea beetle species.

Keywords

Chrysomelidae, Galerucinae, Alticini, biogeography, beetle fossils, taxonomy, phylogeny, insect dispersal

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1. Introduction

Beetles (Coleoptera) are one of the most diverse groups among insects and all Metazoa (Hunt et al. 2007; McKenna et al. 2015). The largest species diversity of beetles is represented by a monophyletic herbivorous clade (so-called Phytophaga, i.e. Chrysomeloidea and Curculionoidea) . Because of this huge diversity, majority of phytophagous beetles, especially in groups, which are not very attractive for amateur entomologists, seems to be still undescribed. One of these groups are also Alticini (Chrysomelidae: Galerucinae), mostly represented by small or medium-sized leaf beetles. Their English name ‘flea beetles’ refers to their typical behavioral feature – the ability to jump using hind legs with thickened femora and a specialized jumping organ. Jumping provides to flea beetles a perfect way to escape a predator.

The systematic position of flea beetles was reclassified many times during last two centuries, both in their rank (subfamiliar or tribal) and in their phylogenetic status in relation to their closest relatives, the galerucine leaf beetles. The actual view on the problem, based on the modern molecular phylogeny of both groups (Ge et al. 2012) revealed the majority of the Alticini fauna as a monophyletic group, which is a sister group of Galerucinae *s. str*. Surprisingly, few lineages of flea beetles (e. g. *Nonarthra*, *Luperomorpha* or *Hespera*) were recognized as internal lineages inside of the galerucine clade, where the jumping ability originated as a convergence.

Flea beetles are distributed worldwide (with exceptions of Antarctica and some oceanic islands). Although the knowledge about the historical biogeography of the group is very limited, partly by the absence of phylogenetic data, there are some preliminary studies, showing cases of colonization and radiation on islands (D’Alessandro et al. 2014; D’Alessandro et al. 2016), distributional patterns on continents corresponding to phylogenetic position of particular groups (Biondi & D’Alessandro 2012) or biogeographic events corresponding to paleogeographical reconstructions (e.g. the Great American Interchange or crossing the Wallace’s line; Mohamedsaid 2009; Scherer 1988).

In this thesis, I summarize basic information about flea beetle evolution, discuss the traits in morphological, ecological or karyotypic evolution mentioned in the literature, and present some insights into the historical biogeography of the group. I also discuss some interesting aspects of flea beetle biology, e.g. the species inhabiting forest leaf litter and the corresponding loss of flight abilities. I specify and discuss future research possibilities in the biology, evolutionary systematics and historical biogeography of flea beetles, in connection to my future MSc. project.

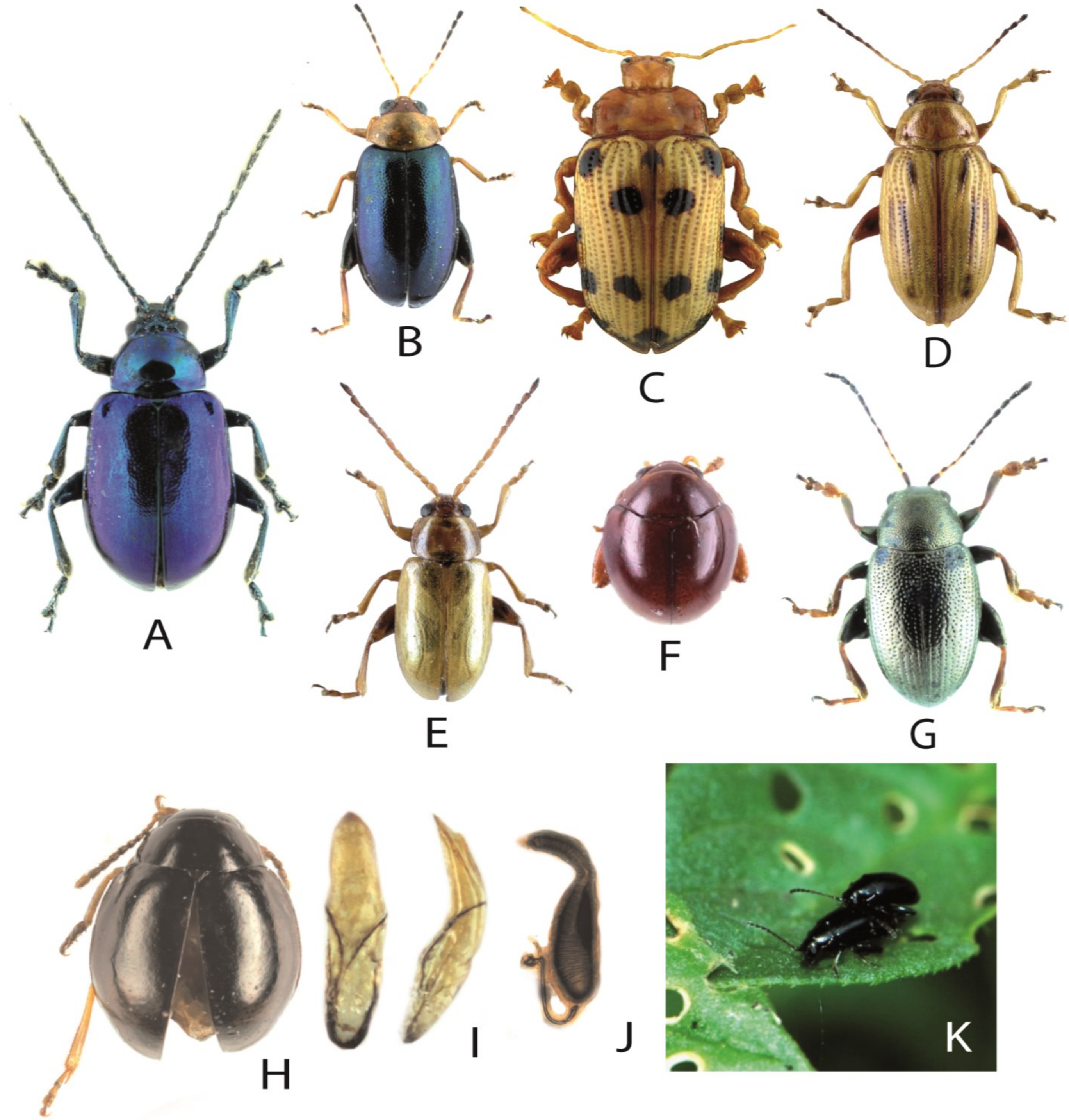

Fig. 1. – Examples of flea beetles. *A – Altica birmanensis* (Jacoby, 1896), Thailand – Doi Inthanon; B – *Hyphasis cyanipennis* (Motschultsky, 1866), Thailand – Doi Inthanon; C – *Podontia quatuordecimpunctata* (Linnaeus, 1767), Thailand – Phuket; D – *Arrhenocoela lineata* Rossi, 1970, Italy – Fondi env.; E – *Aphthona cyparissiae* (Koch, 1803), Czech Rep. – Hluboká n. Vlt.; F – *Clavicornaltica* sp. nov., Thailand – Khao Sok; G – *Chaetocnema aridula* (Gyllenhal, 1827), Czech Rep. – Havraníky; H – *Cangshanaltica siamensis* Damaška & Konstantinov, 2016, Thailand – Doi Inthanon; I – male aedeagus of *C. siamensis*; I – female spermatheca of *C. siamensis*; K – flea beetles in their environment: *Phyllotreta chotanica* Basu et al. 1981, Thailand – Khlung. Pictures H, I, J are from Damaška and Konstantinov 2016, other pictures original.

2. Evolution and systematics

2.1. History and palaeontology of Chrysomelidae and Alticini

Earliest moments of the leaf beetle evolution still remain unclear. This is caused by a low number of well-preserved and realiably dated fossils limiting our knowledge about morphology and distribution of early Chrysomelidae, but also by methodological problems in using these fossils as calibrations for molecular-based time trees (Toussaint et al. 2016). The latest dated phylogenetic tree of beetles (McKenna et al. 2015) reveals that basal divergences among Chrysomelidae s. str. (excluding Megalopodidae and Orsodacnidae which are members of the cerambycid clade in this phylogeny) happened during the Early and Middle Cretaceous, ca. between 145 and 105 million years ago (Ma). Divergence of Galerucinae and Chrysomelinae is considered to take place about 110 Ma. The study by Toussaint et al. (2016) suggests an alternative calibration of McKenna's (2015) tree using a higher number of reliably identified and dated fossils, which pushes the divergence time of Chrysomelidae to the Late Triassic to Early Jurassic, between 222 and 187 Ma.

As mentioned above, the Mesozoic fossil record of leaf beetles is very poor. Older literature (Santiago-Blay 1994) lists relatively many fossil chrysomelid taxa from the Mesozoic, but the identity of most of them is unclear and/or highly speculative because the fossils are badly preserved, insufficiently described and sometimes even lost. Other fossils were misidentified at first and their position in Chrysomelidae was denied by further studies. This is the case of Protoscelinae, a group of Mesozoic beetles originally placed into Chrysomelidae, considered to be the only extinct leaf beetle subfamily (Santiago-Blay 1994). Nevertheless, modern studies transferred the whole subfamily Protoscelinae into the Anthribidae, i.e. out of Chrysomeloidea (Legalov 2013), although additional studies seem to be needed to corroborate this position (S. Davis, pers. comm. to M. Fikáček, 2016). Fortunately, there are some well-preserved fossils of leaf beetles from the Mesozoic, e. g. *Mesopachymerus antiquus* Poinar, 2005[1], a bruchine from Canadian amber of Cretaceous origin (Poinar 2005). The oldest fossils considered as Chrysomelidae are members of the extinct tribe Mesolpinini, described from compression fossils found in the Lower Cretaceous of Liaoning, China and placed into the subfamily Chrysomelinae (Kirejtshuk et al. 2015). No reliable fossils of a flea beetle are known from the Mesozoic. The only known fossil which could possibly belong to Alticinae is a very old record (Westwood 1854), identified as *"*a minute *Haltica* or other Chrysomelideous beetle*"*. However, pictures in the work of Westwood (1854) do not allow a modern interpretation of this fossil and the material was not examined by modern authors.

After the K/T boundary, the number of known leaf beetle fossils increases rapidly, probably due to the existence of large amber deposits, especially in the Baltic area (Eocene) and the Dominican

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[1] The species is originally described as *Mesopachymerus antiqua*, but this name is invalid because of a wrong latin spelling (the generic name is masculine, instead of the feminine form of the species name). Therefore, I am spelling the species name as a masculine too.

Republic (Miocene) (Bukejs 2015; Nadein 2010; Moseyko et al. 2010; Rasnitsyn & Ross 2000). Fifteen species of fossil flea beetles in 9 genera are described up to date from Tertiary fossil resins and it is likely that many other new alticine fossils will be found in the future (Biondi 2014; Bukejs et al. 2015; Nadein et al. 2016; Bukejs et al. 2016). Three recent genera are known also from fossil resins (*Crepidodera* Chevrolat, 1836*, Neocrepidodera* Heikertinger, 1911 and *Wanderbiltiana* Bechyně, 1955). The number of fossils (and sub-fossils) of flea beetles increases during the Neogene and, especially, Quaternary again. The Quaternary fossils and subfossils mostly belong to recent genera (e. g. *Altica* Geoffroy, 1762*, Hippuriphila* Foudras, 1861*, Chaetocnema* Stephens, 1831) (Santiago-Blay 1994; Kuzmina 2015; Buckland & Buckland 2012).

Fossil resin inclusions (the only relevant Paleogene flea beetle fossils) show us some interesting information about Paleogene flea beetle fauna:

(1) European Eocene amber fossils include taxa related to modern Oriental lineages. This is the case of the extinct genus *Manobiomorpha* possibly related to recent Oriental genera *Lipromima* and *Manobia*, both Oriental (Nadein et al. 2016). It corresponds with the findings in other groups (e. g. trees or mammals) in which the current Paleotropical endemics were present in European paratropical and subtropical Cenozoic landscape (Kemp 2005; Nadein et al. 2016). An interesting case, corresponding with this problem, is represented by the recent European endemic flea beetle *Arrhenocoela lineata* (Rossi, 1719). Taxonomic position of this flea beetle is very unclear and it is supposed that it is related to *Xuthea* Baly, 1865 from the Oriental region. This would suggest that *A. lineata* may be a relict of tropical fauna distributed in Europe during the Cenozoic (Biondi & De Nardis 2002). However, *A.lineata* was not incorporated in any molecular phylogeny and the hypotheses need to be addressed once the phylogenetic position of the genus will be clear.

(2) Although tropical species are found in Baltic amber, members of temperate faunal elements (e. g. *Crepidodera, Psyllototus*) prevail in the Eocene fauna. This shows that Baltic amber is a record of a seasonal paratropical forests with warm summers and mild winters where both tropical and temperate animals could live and co-occur (Nadein et al. 2016).

(3) An interesting case is presented by a newly published study (Konstantinov 2016) describing a new recent flea beetle genus *Chanealtica* Konstantinov, 2016, which is very similar to the fossil genus *Psyllototus* Nadein, 2010 from European Eocene amber deposits (Nadein et al. 2016). Both genera are very similar to *Psylliodes* Latreille, 1829, a widespread flea beetle genus, characterized by the combination of 10 antennomeres and the metatarsus attached far from metatibial apex. The second character is typical also for other genera (*Aphthonoides* Jacoby, 1885*, Argopistes* Motschultsky, 1860*, Metroserrapha* Bechyně, 1950, slightly also for the group Monoplatina), but is rare among other flea beetles. The fossil *Psyllototus* is very similar to and possibly closely related to *Psylliodes*, but differs in having 11 antennomeres (Nadein 2010). The newly described recent *Chanealtica* is also very similar to *Psylliodes* and also has 11 antennomeres, which is why its close relation with *Psyllototus* was suggested (Konstantinov 2016). However, a biogeographic problem occurs in the hypothesis –

Psyllototus is known only from European amber, whereas *Chanealtica* is described from Chile. *Psylliodes* is a cosmopolitan genus. Molecular phylogenetic analysis revealing the position of *Chanealtica* would be necessary for clarifying this problem.

A checklist of known fossil Alticini.

Only data with some generic determination are involved – obsolete fossil findings of "incertae sedis" or "Altica sp." are neglected, with exception of the Jurrasic species described as Altica sp., which needs to be revised, but interestingly, it is the only known fossil of suspect alticine from the Mesozoic.

Review literature: Kirejtshuk & Ponomarenko (2017); Santiago-Blay (1994); Nadein et al. (2016); Bukejs & Nadein (2013).

Mesozoic fossils.

***Altica* sp. (in: Westwood 1854)**
Jurassic, Durdlestone Bay, England
Remarks: The fossil had not been redescribed and is originally determined as „Haltica or other Chrysomelidan".

Tertiary fossils.

***Altica dryophyllorum* Piton, 1940**
Paleocene, Menat, Puy-de-Dome, France

***Altica dubia* Foerster, 1891**
Oligocene, Brunnstatt, Elsas, France

***Altica magna* Foerster, 1891**
Oligocene, Brunnstatt, Elsas, France

***Altica renovata* Wickham, 1941**
Oligocene, Florissant, Colorado St., USA

***Altica* sp. (in: Helm 1896)**
Eocene, Baltic amber

***Acallepitrix* sp. (in: Santiago-Blay&Craig 1999)**
Miocene, Dominican amber

***Altica tholimorpha* Zhang et al., 1994**
Miocene, Shanwang Basin, Shandong Prov., China

***Ambroaltica baltica* Bukejs et Konstantinov, 2013**
Eocene, Baltic amber

***Aphthona puncticollis* Piton, 1939**
Miocene, Cantal, Murat, France
Remarks: Unclear generic placement, needs revision.

***Apteropeda grossa* Theobald, 1937**
Miocene, Cantal, Murat, France
Remarks: Unclear generic placement, needs revision.

***Archealtica convexa* Nadein, 2016**
Eocene, Rovno amber, Ukraine

***Crepidocnema yantarica* Moseyko et al., 2010**
Eocene, Oise amber, France

***Crepidodera decolorata* Nadein et Perkovsky, 2010**
Eocene, Rovno amber, Ukraine

***Crepidodera svetlanae* Bukejs, 2014**
Eocene, Baltic amber

***Crepidodera tertiotertiaria* Bukejs et al., 2016**
Eocene, Baltic amber

***Derorthea curtiantenna* Zhang et al., 1994**
Miocene, Shanwang Basin, Shandong Prov., China

***Manobiomorpha eocenica* Nadein, 2010**
Eocene, Rovno amber, Ukraine

***Neocrepoidodera antiqua* Gressit, 1970**
Miocene, Chiapas amber, Mexico

***Ochrosis* sp. (in: Klebs 1873)**
Eocene, Baltic amber

***Oryctoscirtites protogaeum* Scudder 1876**
Oligocene, Florissant, Colorado St., USA

***Paolaltica eocenica* Biondi, 2014**
Eocene, Baltic amber

***Phyllotreta* sp. (in: Kiselev 1981)**
Pliocene, Siberia

***Plectrotetrophanes hageni* Wickham, 1914**
Oligocene, Florissant, Colorado St., USA

***Prochaetocnema florissantella* Wickham, 1914**
Oligocene, Florissant, Colorado St., USA

***Psylliodes difficilis* Foerster, 1891**
Oligocene, Brunnstatt and Kleinkembs, Alsace-Lorraine, France

***Psylliodes difiguratus* Theobald, 1937**
Oligocene, Kleinkembs, Baden-Wurtemberg, Germany

***Psyllototus doeberli* Bukejs et Nadein, 2013**
Eocene, Baltic amber

***Psyllototus groehni* Bukejs et Nadein, 2014**
Eocene, Baltic amber

***Psyllototus progenitor* Nadein, 2010**
Eocene, Rovno amber, Ukraine

***Psyllototus viking* Nadein et al., 2016**
Eocene, Danish amber

***Sucinolivolia torpida* Bukejs et al., 2015**
Eocene, Baltic amber

***Systena florissantensis* Wickham, 1914**
Oligocene, Florissant, Colorado St., USA

***Walterianella* sp. Santiago-Blay et al., 1996**
Miocene, Dominican amber

***Wanderbiltiana wawasita* Santiago-Blay et al., 2004**
Miocene, Dominican amber

2.2. Phylogenetic position and systematic status of Alticini

Chrysomelidae are a diverse family of beetles (Coleoptera), placed into the clade Chrysomeloidea. The sister group of Chrysomeloidea is Curculionoidea (weewils and their relatives), together, this megadiverse phytophagous clade is informally known as Phytophaga and is nested in the series Cucujiformia (Haddad & McKenna 2016; McKenna et al. 2015). Chrysomelidae are a monophyletic family (Hunt et al. 2007; McKenna et al. 2015; Gómez-Zurita et al. 2008; Haddad & McKenna 2016). A discussion was taken during last decades about the phylogenetic positions of Megalopodidae and Orsodacnidae, groups formerly recognized as subfamilies of Chrysomelidae. Afterwards, both groups were designated as separate families and hypothetically placed as sister clades of Chrysomelidae. However, modern molecular phylogenies uncovered their relation with Cerambycidae, which is also supported by presence of a stridulatory organ between head and pronotum, which now appears to be a synapomorphy of the "cerambycid clade". An antagonistic situation happened with the former family Bruchidae. This group is recently considered as a subfamily of Chrysomelidae, which is based both on larval morphology and molecular data (Gómez-Zurita et al. 2008; Bouchard et al. 2011). Recent studies indicate their relation with the chrysomelid subfamily Sagrinae.

Phylogenetic relationships among subfamilies of Chrysomelidae are revealed by several molecular studies (Gómez-Zurita et al. 2008; Gómez-Rodríguez et al. 2015). The tree of Gómez-Zurita et al. (2008) is presented on the Fig. 2. Chrysomelidae form three main clades – the Sagrine clade (containing Donaciinae, Criocerinae, Bruchinae and Sagrinae), the Chrysomeline clade (containing Chrysomelinae and Galerucinae, where Chrysomelinae split up into two clades) and Eumolpine clade (containing the rest of leaf beetle subfamilies – Spilopyrinae, Eumolpinae, Cassidinae, Lamprosomatinae and Cryptocephaline groups Clythrinae, Cryptocephalinae and Chlamysinae). Eumolpines are, surprisingly, paraphyletic. Actual phylogeny by Gómez-Rodríguez et al. (2015), is not using a sampling wide enough to reject the results of Gómez-Zurita (2008) and a review by Haddad and McKenna (2016) shows that relationships and monophyly of several chrysomelid lineages

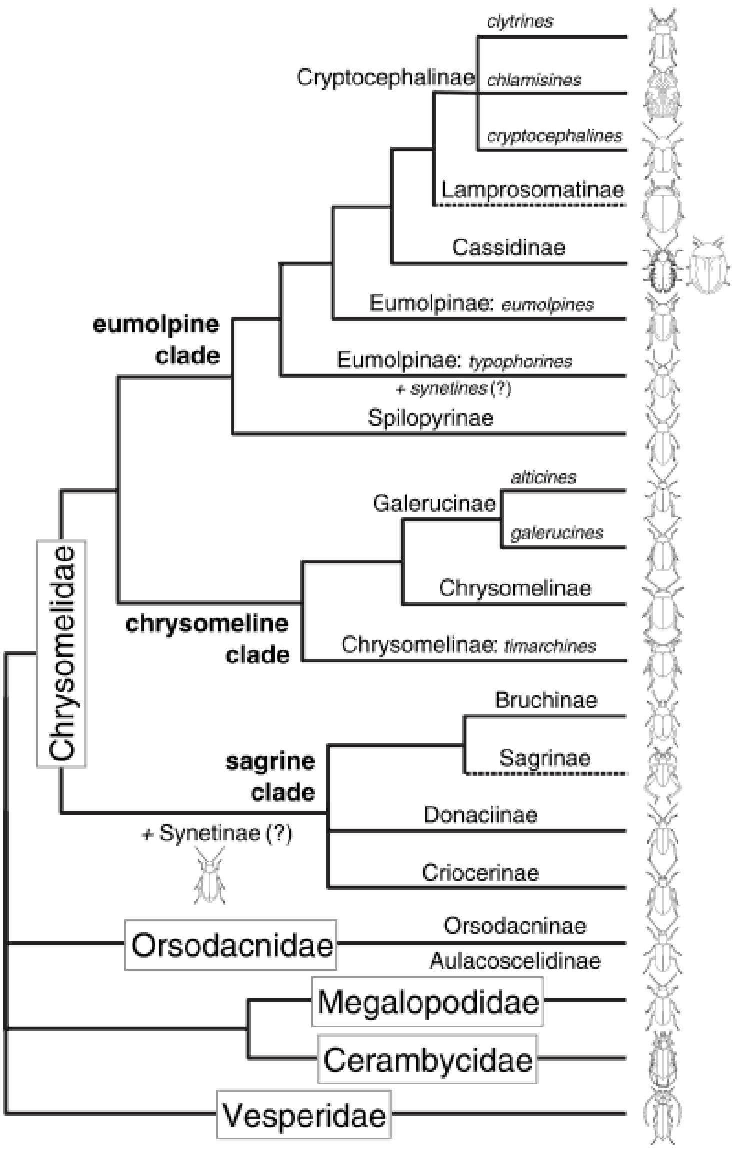

Fig. 2 – a tree of the Chrysomelidae family based on multilocus ribosomal RNA phylogeny by Gómez-Zurita et al. (2008).

(especially the cryptocephaline lineages, eumolpines and chrysomelines) still unclear. Nevertheless, the Galerucine-Alticine clade (Galerucinae s. lat.) is monophyletic in all cases.

A problematic point is the division of these two groups. Flea beetles were traditionally considered as a separate subfamily Alticinae (Seeno & Wilcox 1982; Konstantinov & Vandenberg 1996). However, a close link between Alticinae and Galerucinae permanently proposed a possibility that Alticinae are an internal lineage of Galerucinae – this opinion was also presented in some old systematic works (Chapuis 1875; Horn 1889). Several phylogenies were published on this problem with confusingly variable results. a phylogeny by Lingafelter and Konstantinov (1999) based on 50 adult morphological characters revealed a hypothesis of paraphyletic Galerucinae and Alticinae as a lineage within Galerucinae. The authors propose a nomenclatorical rearrangement and design the tribe Alticini within Galerucinae. Interestingly, the alticine clade was in the phylogeny by Lingafelter and Konstantinov (1999) nested within the galerucine tribe Luperini, which has root-feeding larvae, a typical character for majority of alticines. A problem of this phylogeny is low taxon sampling, which is also discussed by the authors. On the contrary, other studies (Reid 1995; Crowson & Crowson 1996) propose a completely different hypothesis: Alticinae are paraphyletic and Galerucinae are a lineage within Alticinae. This hypothesis would indicate that the common ancestor of galerucines completely lost its metafemoral spring – a structure connected with jumping present in all alticines (see Chapter 3.2). However, Reid (1995) proposes the loss of the metafemoral spring is possibly an easy evolutionary event. The third possible hypothesis, proposed by a study made during this “wild time" of many contradictive hypotheses, is the monophyly of both Alticinae and Galerucinae, based on the analysis of an 18S single gene phylogeny of Phytophaga (Farrell 1998). However, a low taxon sampling of both galerucines and alticines is again a problem in this analysis and the support for this hypothesis is therefore low. All hypotheses from the "wild time" are discussed by Kim et al. (2003), who compares all of them and improves the morphological dataset from Lingafelter and Konstantinov (1999) by three partial gene sequence data. The result of the analysis is a confirmation of the "monophyletic Galerucinae hypothesis" – Alticinae are paraphyletic and galerucines form a monophyletic clade within, which lost the metafemoral spring. Another three-gene molecular phylogeny by Bünnige et al. (2008) reveals a similar phylogenetic tree – Alticinae are paraphyletic again, with galerucines nested inside.

A new view into the problem was presented by a multigene sequence phylogenetic analysis by Ge et al. (2011). This analysis is not ground-breaking only because of the usage of a relatively good molecular dataset – it is also the first study, where a relatively wide sampling of taxa among galerucines (more than 100 genera) and alticines is involved. Four genes (two mitochondrial and two nuclear) were used on a large sample of Alticinae and Galerucinae, and the presence and morphology of the metafemoral spring was mapped on the topology. The subfamily Galerucinae s. lat. appears to consist of two main diverse groups, where one of them contains nearly all flea beetles included in the study and no non-jumping galerucines. The second clade of Galerucinae s. lat. contains all non-jumping galerucines in the study, but surprisingly also five lineages of jumping galerucines, previously classified as Alticinae. The same situation happened in the subsequent phylogenetic analysis of Galerucinae s. lat. (Ge et al. 2012), which used different methods of alignment and more precise phylogenetic analysis on the same dataset. The newest relevant phylogenetic tree of Galerucinae s. lat. is presented in Fig. 3.

Another contribution to the discussion is a recent phylogenetical study by Hua et al. (2014), which is strictly morphological and based on larval characters. The tree containing a really small sample of alticines and a better, but still extremely incomplete sample of galerucines, reveals a confusing situation – both lineages are polyphyletic. Galerucines are considered to be a lineage inside a radiation of alticines and a monophyletic *Blepharida*-group is nested within the galerucine clade. This topology is evidentely confused and irrelevant, which is also confessed by the authors as an artifact of a low taxon sampling. Some partial phenomena, including monophyly of Luperini, Oidini, Hylaspini and the *Blepharida*-group, are nonetheless interesting and can demonstrate that larval morphology could be a potential source of phylogenetically significant characters. However, the study is not very relevant in solving the "alticine-galerucine problem".

The phylogeny by Ge et al. (2012), which is probably the most relevant alticine-galerucine phylogeny, shows, that there are no relevant arguments to classify Alticinae as a tribe Alticini in the family Galerucinae – especially if the nomenclature is designed in the way of dividing Galerucinae into two tribes (Alticini and Galerucini). This treatment, in my opinion, is not necessary, makes no change in systematics and causes confusion. The most relevant nomenclatorical treatment of the group could be designating two subfamilies: (1) Galerucinae, divided into traditional tribes (Luperini, Galerucini etc.) and containing all known jumping lineages, where the jumping ability was considered to be convergent to the jumping ability of true alticines, and (2) Alticinae as a monophyletic sister group of Galerucinae with the jumping ability as a key synapomorphy. However, in accordance with recent usage in the literature (Bieńkowski and Orlova-Bienkowskaja 2016; Biondi, Urbani, and D'Alessandro 2013; Biondi 2014; Hua et al. 2013; Lee et al. 2011; Ruan et al. 2015), I respect flea beetles as a tribe Alticini inside the subfamily Galerucinae, with reservations discussed below.

2.3. Suprageneric classification of flea beetles

Despite the big diversity of flea beetles, there is no often-used tribal (or subtribal) systematics of the group. New genera are usually described with discussions of which genera are possibly closely related, but formally, they are described as *incertae sedis* and not placed to any tribe or genus group. Nevertheless, there were some trials to designate the suprageneric flea beetle system, which are a crucial source for further systematics.

The first suprageneric system of flea beetles was created by Chapuis (1875), who designated 19 subtribes. Horn (1889) modified the system, focusing on American genera. However, modern catalogues (Döberl 2010; Mohamedsaid 2016; Biondi & D'Alessandro 2012) do not use any system for cataloguing alticine genera. Scherer (1983) does not name the majority of genus-groups, except of two tribes, Oedionychini and Monoplatini. These two tribes (or subtribes) are usually the only named suprageneric taxa even in recent literature (Konstantinov & Konstantinova 2011; Casari & Teixeira 2011).

Seeno & Wilcox (1982) vote a 'buck-passing' statement – they do not name groups of genera in their catalogue, but they present some possibilities of the tribal classification and classify genera into some groups, where nominate genus for each group is marked. However, they state that systematics of alticines needs to be clarified. Bouchard et al. (2011) lists some subtribal names in Alticini, but a majority of them is not used. Takizawa (2005) tries to divide flea beetles into suprageneric taxa using larval morphology characters. Although he newly describes some Neotropical alticine larvae, the systematics is still very incomplete and biased on eastern Palearctic and Oriental fauna. He states that his larval system is incomplete and compares it with the systematic attempts by Seeno & Wilcox (1982), which he states as *adult morphology groups*. According to Takizawa's study, larval morphology is usable for suprageneric systematics in some cases and we can see some apomorphies there (e. g. in Takizawa's 'Hemipyxis group', which corresponds with usually recognized subtribe Oedionychina). In other cases, larval morphology shows to be highly homoplastic (e. g. in cases of leaf miners, which have very similar larval morphology according to their special life style). Another case of confusion is represented for example in the Takizawa (2005) *Liprus* group, which contains genera, listed in totally different groups by Seeno & Wilcox (1982) and Chapuis (1875). Takizawa (2005) states his study as an evidence of a possibly good contribution of larval morphology to the problem of suprageneric alticine systematics. According to the previously mentioned paper by Hua et al. (2014), I can agree that larval morphology can be very useful in searching some apomorphies for specific subgroups, but definitely, it cannot be used as a key source for uncovering alticine phylogeny.

Another contribution to supregeneric systematics of flea beetles was done by studying the morphology of the metafemoral extensor tendon ('metafemoral spring'), which are discussed in the Chapter 3.2. Here I only mention that the morphology of the metafemoral apodeme appears to be highly homoplastic in general, but it can be helpful for morphological treatment of some genus-groups, because in some cases, closely related genera bear a similar type of the metafemoral extensor tendon (Ge et al. 2011; Ge et al. 2012; Furth & Suzuki 1998).

The newest contribution in alticine suprageneric systematics is the previously mentioned paper by Ge et al. (2012), which is a crucial modern work in flea beetle evolution and systematics. 18 species groups, based on well-supported nodes on a phylogenetic tree were designated in this paper. Many of these groups correspond relatively with morphologically defined subtribes by Chapuis (1875), e. g. Blepharida group (Blepharidites in Chapuis 1875), *Amphimela* group (Amphimelites in Chapuis 1875), *Oedionychis* group (Oedionychites in Chapuis 1875) or *Monoplatus* group (Monoplatites in Chapuis 1875). Other traditional morphological groups by Chapuis (1875) split into more unrelated genus groups, e. g. the Aphthonites by Chapuis (which is newly considered as a group containing only *Aphthona* and some very related genera, but not *Longitarsus* or *Phyllotreta*, which are not related to Aphthonites) or Mniophilites by Chapuis, which represent a wastebasket taxon of many unrelated genera of oval and convex body shape. Three named genus-groups (*Luperomorpha* group, *Nonarthra* group and *Hespera* group) were transferred into Galerucinae (or Galerucini s. str.), another two recognized saltative lineages were considered as members of Sermylini (Galerucinae s. str.).
A problematic point of the study is the designation of the '*Chaetocnema* group', which is paraphyletic and includes the *Altica* group. All other designated genus-groups are monophyletic. Many important genera were not included into any genus-group and stay incertae sedis, waiting for further more comprehensive and complex phylogenetic study. An interesting point of the study is for example a possibly isolated position of the genus *Systena*. However, the support for the *Systena* – branch is not very big. The biggest problem of the study is in the geographically biased sampling – the majority of sampled genera are Palearctic and, especially, Oriental genera. Only a few sampled genera (moreover members of well-known groups, as Oedionychina or Monoplatina) are Neotropic and no endemically Afrotropic genus is involved. Also, some problematic genera (as *Crimissa* or *Polyclada*) are not included. Nevertheless, the paper is perfectly usable as a basal work and a keystone of modern flea

beetle systematics, because new genes and new taxa can be easily added into the existing phylogeny. A well-working phylogenetically supported and morphologically treated suprageneric systematics of Alticini remains awaiting for further studies.

The table below, comparising various systematics of Alticini, is adopted from (Ge et al. 2012) and complementary data from Furth et al. 1980; 1985; 1988; 1989 and Furth & Suzuki 1998) added additionally.

Chapuis (1875)	**Horn (1889)**	**Takizawa (2005)**	**Furth (1980, 1985, 1988, 1989, 1998)**	**Ge et al. (2012)**
Blepharidites: *Notozona, Blepharida, Ophrida, Podontia*	**Blepharidea**: *Blepharida*	**Podontia group:** *Blepharida, Ophrida, Podontia*	**Blepharida group**: *Amphimeloides, Asialtica, Chabria, Clitea, Erystus, "Lactica", Lipromela, Lypnea, Mellipora, Myrcinoides, Ophrida, Pentamesa, Podagricomela, Podontia, Sinocrepis, Tonfania, Xuthea, Zipangia, Acrotium, Arrhenocoela, Hermaeophaga, Mantura, Podagrica, Cacoscelis, Crimissa*	***Blepharida* group**: *Blepharida, Ophrida, Podontia*
Elithiites: *Elithia, Crimissa*				
Diamphidiites: *Diamphidia*				
	Euplectrosceles: *Euplectroscelis*			
Arsipodites: *Arsipoda, Nisotra, Podagrica, Balanomorpha*	**Arsipodes**: *Mantura*			***Nisotra* group**: *Euphitrea, Sinocrepis, Podagrica, Nisotra Sphaeroderma,*
Amphimelites: *Amphimela*		**Clitea group:** *Clitea, Crepidodera, Hippuriphila, Lythraria*		***Amphimela* group**: *Amphimela, Podagricomela, Clitea*
				***Manobia* group**: *Manobia, Aphthonoides, Asiorestia, Lythraria*
Halticites: *Haltica, Pelonia, Phrynocepha, Caeporis Plectrotetra, Cacoscelis, Disonycha, Caloscelis,*	**Halticae:** *Haltica*	**Altica group:** *Lysathia, Aphthona, Macrohaltica, Altica, Neocrepidodera, Othocrepis*	**Altica group:** *Neodera, Altica, Neocrepidodera, Trichaltica, Crepidodera, Derocrepis, Disonycha, Epitrix, Hemiglyptus, Hippuriphila, Hornaltica, Luperaltica, Lysathia, Lythraria, Syphrea Macrohaltica, Minota, Cardax, Mniophila, Monomacra, Ochrosis, Phrynocepha, Strabala,*	***Altica* group**: *Altica, Macrohaltica, Syphraea*
Aphthonites: *Longitarsus, Phyllotreta Glyptina, Botaphila, Aphthona*	**Aphthona:** *Aphthona, Phyllotreta Longitarsus, Glyptina*			***Aphthona* group**: *Aphthona, Aphthonomorph, Glyptina*

			Phyllotreta group: *Phyllotreta, Apraea, Aphthonaltica, Manobia, Pedethma, Xenidea, Suthrea, Yunohespera, Dysphenges, Glenidion, Lupraea, Pachyonychus, Phydanis, Pseudolampsis, Systena, Exoceras, Pedilia, Hemilactica, Homoschema Phydanis,*	
Lacticites: *Lactica, Diphaulaca, Hermaeophaga, Xuthea Psilapha, Myrcina,*	**Lactica**: *Lactica, Diphaulaca, Trichaltica*			***Lactica* group**: *Hermaeophaga*, *Lactica*, *Orthocrepis*
	Disonychae: *Disonycha, Hemiphrynus*			***Disonycha* group**: *Diphaltica*, *Agasicles*, *Disonycha*
		Longitarsus group: *Longitarsus*	**Longitarsus group:** *Longitarsus*	***Longitarsus* group**: *Lanka*, *Longitarsus*, *Tegyrius*
		Lanka group: *Lanka*		
Crepidoderites: *Pseudodera, Systena, Clamophora, Tenosis, Crepidodera, Prasona, Iphitrea*	**Chaetocnemae**: *Chaetocnema*	**Chaetocnema group**: *Chaetocnema*	**Chaetocnema group:** *Anthobiodes, Aphthona, Argopus, Asphaera, Capraita, Euplectroscelis, Glyptina, Heyrovskya, Kuschelina, Oedionychus, Pachyonychis, Alagoasa Sphaeroderma, Chaetocnema, Bhamoina, Halticorus, Eucyclomela, Hyphasis, Lipromima,*	***Chaetocnema* group**: *Psylliodes*, *Chaetocnema*, *Crepidodera*
Plectroscelites: *Chaetocnema (*as *Plectroscelis*)				
	Systenae: *Systena*			
	Crepidoderae: *Hemiglyptus Epitrix, Crepidodera, Orthaltica, Leptotrix*			
Psylliodites: *Psylliodes*	**Psylliodes**: *Psylliodes*	**Liprus group:** *Liprus, Phygasia, Phyllotreta, Pseudodera, Psylliodes, Sangariola*	**Psylliodes group**: *Psylliodes, Schenklingia, Goweria, Arsipoda, Aphthonoides, Megistops,Apteropeda, Argopistes, Batophila, Dibolia, Distiogmoptera, Aedmon, Heikertingerella*	***Pseudodera* group**: *Pseudodera*, *Laboissierea*
				***Phygasia* group**: *Phygasia*, *Trachyaphthona*
			Sangariola group: *Liprus, Sangariola, Laboissierea, Pseudodera*	
Diboliites: *Dibolia, Megistops*	**Dibolia**: *Dibolia*	**Sphaeroderma group:** *Argopistes, Argopus, Dibolia, Megistops Schenklingia, Sphaeroderma*		***Dibolia* group**: *Argopistes*, *Dibolia*, *Jacobyana*
Mniophilites: *Mniophila, Argopusa, Hypnophita, Argopistes Sphaeroderma, Apteropeda,*	**Mniophilae:** *Argopistes, Sphaeroderma*			
				***Pentamesa* group**: *Pentamesa*, *Bhamoina Argopus*

				***Chabria* group**: *Chabria*, *Parathrylea*, *Sutrea*, *Chabrisoma*
Oedionychites: *Omophoita, Eutornus, Physodactyla, Oedionychis, Physoma Physonychis, Lithonoma*	**Oedionychis**: *Hamletia, Oedionychis*	**Hemipyxis group:** *Alagoasa, Kuschelina, Walterianella, Philopona Disonycha, Hemipyxis, Omophoita*		***Oedionychis* group**: *Hemipyxis*, *Hyphasis*, *Philopona*, *Physoma*, *Oedionychis,Alagoasa*, *Omophoita*, *Asphaera*, *Wanderbiltiana*, *Aspicela*
Aspicelites: *Aspicela, Sebaethea, Asphaera, Sphaerometopa Rhopalotoma, Febra*	**Aspicelea**: *Homophaeta*, *Phydanis*		**Sphaerometopa group:** *Sphaerometopa*	***Sphaerometopa* group**: *Sphaerometopa* **(Galerucinae)**
Monoplatites: *Monoplatus*, plus 38 genera	**Monoplati**: *Phaedromus*, *Pachyonychus*, *Hypolampsis*			***Monoplatus* group**: *Monoplatus*
	Pseudolampses: *Pseudolampsis*			
		Pseudoliprus group: *Pseudoliprus, (Mantura)*	**Pseudoliprus group:** *Pseudoliprus, Lipromorpha*	
			Chalaenosoma group: *Chalaenosoma, Luperomorpha*	***Luperomorpha* group**: *Luperomorpha*
Nonarthrites: *Nonarthra*		**Nonarthra group**: *Nonarthra*	**Nonarthra group:** *Nonarthra, Typhodes Glaucosphaera, Trachyaphthona,*	***Nonarthra* group**: *Nonarthra* **(Galerucinae)**
Acrocryptites: *Acrocrypta*			**Acrocrypta group:** *Acrocrypta*	***Acrocrypta* group**: *Acrocrypta* **(Galerucinae)**
Oxygonites: *Oxygona, Chaloenus, Sophraena*				
			Buphonella group: *Chaloenus, Eudolia, Hespera*	**Hespera group:** *Hespera, Laotzeus, Taiwanhespera, Stenoluperus* **(Galerucinae)**
			Mandarella group: *Mandarella, Stenoluperus*	
			Licyllus group: *Licyllus, Thrasychroma*	
			Garuda group: *Garuda*	

As mentioned above, the majority of authors do not place newly described genera into tribal or subtribal classification. However, there are some exceptions, also named above. It is especially the case of the subtribe Monoplatina, which is distributed mainly in the Neotropics. Many new genera, chiefly moss-inhabiting, were assigned to this subtribe during last years (Morais et al. 2016; Konstantinov & Konstantinova 2011; Linzmeier & Konstantinov 2012; Furth 2007). Savini & Escalona (2005) describes a new species of *Longitarsus* and writes about this genus as a member of a tribe Longitarsini.

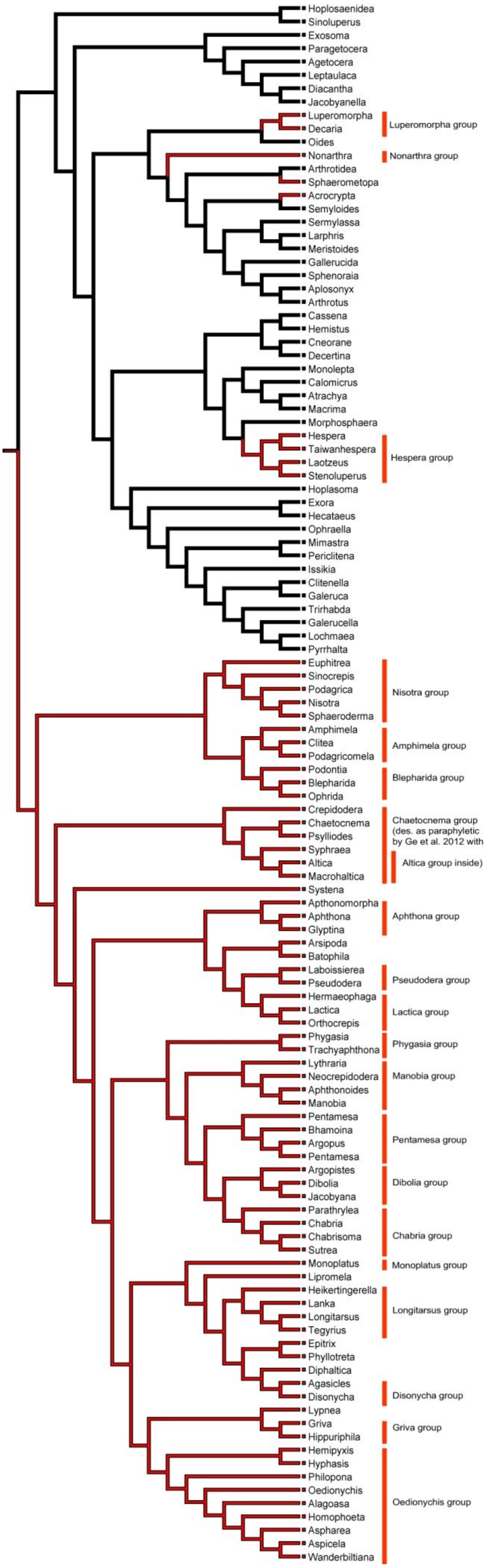

Fig. 3 – An up-to-date phylogenetic tree of Galerucinae. *Black branches: metafemoral apodeme absent, red branches: metafemoral apodeme present. After Ge et al. (2012).*

3. Morphological and Ecological Characters

3.1. Morphological evolution

The evolution of important morphological characters which are often used as diagnostic at tribe-genus levels was analyzed in the work by Ge et al. (2012). A frequent character used for diagnosing flea beetle genera, the presence/absence of the anti-basal transverse impression on the pronotum, appears to be a homoplasy, occurring in many lineages, but not occurring ancestrally. A more interesting case figures the morphology of the procoxal cavities (open or closed), where early-branching clades have a closed procoxal cavity (with few exceptions of lineages in which open procoxal cavities evolved convergentely), but the crown group of Alticini (the sister clade of the *Systena* lineage on the tree) is characterized by open procoxal cavities. Various lineages within this clade then got their procoxal cavities closed again. Further studies should reveal if the morphology of the procoxal cavity has some functional (ecological or kinematic) implications for the beetles. Open procoxal cavity should allow a wider range of movement and deflection of the coxa (and the whole leg). A theory about Cerambycidae supposes it could be an advantage in copulation, because better ability of movement and deflection of the leg can help in attachment of the male on female's body (Perger 2013). However, the closed procoxal cavity should also be advantageous for some reason, as many crown lineages of flea beetles convergentely regained closed procoxal cavity. In my opinion, the closed procoxal cavity (and therefore stronger sclerotization of the body) can be helpful to avoid predator or parasitoid attacks or to survive dry conditions. The analyses by Ge et al. (2012) consider most of the mapped characters as highly homoplastic in general (and hence useless for highler-level systematics), but small subgroups of genera are often well-characterized by some of these apomorphic characters or their combinations. For example, this is the case of the *Blepharida*-group, characterized by the presence of bifid claws. Some groups (*Phygasia*-group and *Disonycha*-group), on the contrary, can be diagnosed only by a combination of plesiomorphies.

An interesting point of morphological evolution of flea beetles is a huge diversity of the shape of hind legs (tibiae and tarsi) present among flea beetle genera. In some cases (e. g. in the genus *Longitarsus*), the tarsus is extremely elongated, in cases of the subtribes Oedionychini and Monoplatini, last tarsal segment forms a maul-like ending, in cases of genera *Psylliodes* or *Chanealtica*, the tarsus is attached nearly in the middle of the tibia and an elongated part of tibia is present behind the tarsus. Also in the case of the genus *Aphthonoides*, there is an extremely long and wide post-tarsal tibial spine. Schmitt (2004) shows that jumping skills of *Longitarsus* are extremely high and this is correlated not only with the shape of the metafemoral extensor tendon (see Chapter 3.2), but also with the absolute length of the hind leg (together with the tarsus), so the elongation of tarsi is an effective specialization for long jumping. Also, the position of the attachment of the tarsi in *Psylliodes*, which is in the middle of metatibia, could be an advantage for jumping efficiency. Photographic studies of the flea beetle jump revealed that the beetle pushes itself from the ground by the apex of the metafemur (Brackenbury & Wang 1995; Nadein & Betz 2016). Therefore, specific structures on the metafemoral apex, as long spines, or the absence of the delicate and vulnerable tibio-tarsal joint can improve the mechanics for the pushing (Konstantinov 2016). The mechanics of the jump in Oedionychina and Monoplatina were not photographed, so we do not know if the pushing mechanism is same as in other flea beetles. Metatibia in Oedionychina are shorter than metafemora (Nadein & Betz 2016), which allows me to speculate that the swollen metatarsi cannot be the main element for pushing the beetle, unlike in other alticines. Also, it can be a tool for changing the focal point of the leg, which can possibly be useful for the jumping efficiency. However, these speculations fundamentally need experimental verification.

3.2. Jumping ability

The ability to jump presents the major diagnostic character, on which pre-phylogenetic taxonomical diagnosis of flea beetles was based. The first contribution to the knowledge of the function of jumping abilities of flea beetles was made by Maulik (1929), who described a specific chitinized organ in the inner space of the extended metafemur, and a number of strong muscules connected with this structure, the metafemoral wall and the tibia. Maulik (1929) suggests that this organ should be responsible for jumping, because it is found in all alticine species he examined. He proposes the presence of this structure as a diagnostic character for distinguishing Alticinae and Galerucinae, because it is found also in non-jumping species of Alticinae (e. g. *Podontia* sp.), which shows that ancestors of these species had the ability to jump which was later lost. Lever (1930) uncovered another independent chitinized structure in the anatomy of the metafemur – a small subtibial triangular plate. Barth (1954) describes on a model species *Homophoeta sexnotata*, how the jumping mechanism could work: the inner chitinized organ functions as a medium for accumulation of the energy by its extension by the muscules. The relaxation of the muscules provides contraction of the chitinized organ and adduction of the tibia. This theory was corroborated by further studies by (Furth et al. 1983; Furth 1988) which aimed on finding an exact mechanic background of the function of the metafemoral spring, how the chitinized organ was named by Furth (1988). The major effort was invested in finding the evidence for the presence of resilin in the metafemoral spring. Resilin is a special, extremely elastic protein. It is widespread among insects in their jumping organs, e. g. in Siphonaptera , Hemiptera and also numerous Coleoptera (Burrows et al. 2008; Michels et al. 2016; Lyons et al. 2011). Resilin was also discovered in beetle wing veins (Haas et al. 2000), where it improves the elasticity, in compound eyes, where it is probably present due to its very good optical properties, and in a plenty of other functions in all arthropods (Michels et al. 2016). However, resilin was not found in the ultrastructure of the metafemoral spring, which consists from alpha-chitin and protein fibers. However, Furth et al. (1983) assumes that even without resilin the chitinous and protein structure itself provides good elastic properties for accumulation of the jumping energy. Neverthless, a recent study (Nadein & Betz 2016) shows that the interpretation of the metafemoral spring as an energy storage mechanism was completely false. The authors used various methods to explain flea beetle jump, including hi-tech methods such as synchrotron imaging. They tried to search resilin fibres not only in the metafemoral spring, but also in the other parts of the metafemur, which was successful – because of blue autofluorescence of resilin, fluorescence microscopy uncovered massive presence of resilin in the extensor ligament, a short connection between the metafemoral spring and the tibia, in some other ligaments and in joint membranes of the femoro-tibial joint.

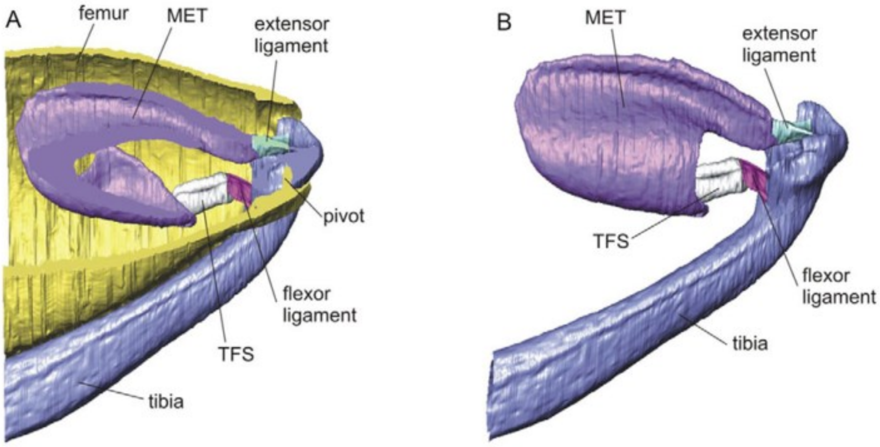

***Fig. 4 – Morphology of the metafemoral extensor tendon** of* Sphaeroderma testaceum *by Nadein & Betz (2016). A – a picture with a cut through the metafemoral cuticle; B – a picture with the metafemoral cuticle removed. MET – metafemoral extensor tendon, TFS – tibial flexor sclerite (Lever's triangular plate).*

In the contrary, the metafemoral spring does not show any special elastic properties. This leads to the confidence that the metafemoral spring can store minimum of the energy needed for the jump (maximally 10 %) and the major energy-storage mechanism is represented by the resilinized ligaments and membranes. The presence of the metafemoral spring is, nevertheless, fully correlated with the jumping ability, so its role in the jumping should be crucial. The authors of the study suggest that the function could be in providing a massive space for connecting flexor musculature – the metafemoral spring can be a "handle" for flexor muscles. The role of the Lever's triangular plate (Fig. 3) might be protective, it strengthens the base of the flexor tendon and provides also a larger angle for flexing the tibia by "diving" into the tibial cavity during the flexing of tibia (and stretching the extensor ligament). It can also help in prevention of a premature extension of the tibia. The authors re-name the metafemoral spring to the metafemoral extensor tendon, because, according to their results, it actually does not function as a spring. The anatomic visualization of the jump is presented on Fig. 5.

Although the metafemoral extensor tendon is not direct energy storage, its morphology is significant for phylogenetic studies. It is present among more families and subfamilies of beetles, e. g. weewils

(Rhynchaeninae, Erirhininae, Ceutorhynchinae), Melandryidae, Scirtidae, Anthribidae, Buprestidae etc. and also in one other subfamily of leaf beetles, Bruchinae (Furth & Suzuki 1992).

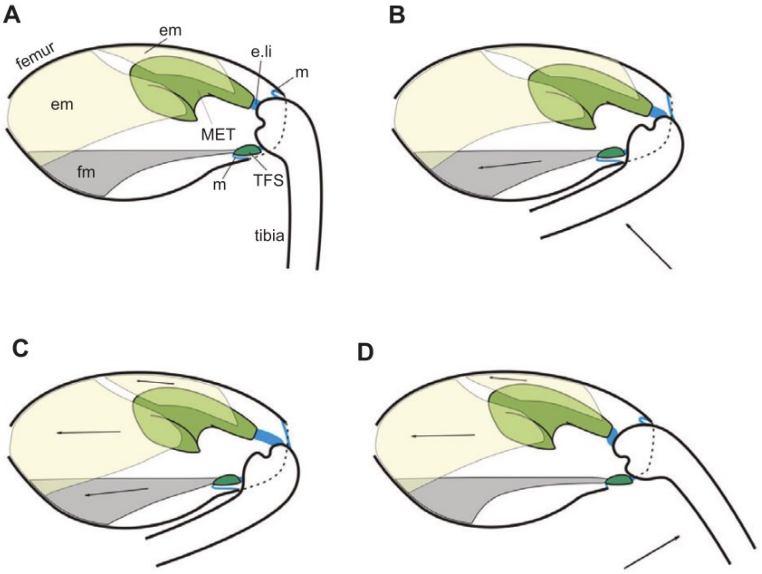

Fig. 5. – A jump of a flea beetle: how does it work. *a – initial phase, B – prior flexion of the tibia, C – flexion of major femoral flexor muscles and tension of the resilinized extensor ligament, D – relaxation of the tibial flexor, flexion of the extensor ligament, flexion of big flexor muscles for maximizing the extension of the tibia: the take-off. Anatomical legend to A: em – extensor muscles, fm – flexor muscles, MET – metafemoral extensor tendon, TFS – Lever's trinangular plate, m – membrane, e.li – extensor ligament. Figure from Nadein & Betz (2016).*

Furth (1988) tries to define 6 morpho-groups based on the morphology of the metafemoral extensor tendon (MET). He assumes that intrageneric variability of the MET is low, but describes a relatively high intergeneric variability. He also assumes flea beetles as a monophyletic group based on the presence of the metafemoral extensor tendon and other aspects of their unique evolution, which are, however, not defined in the paper. In further studies (Furth & Suzuki 1998), additional genus-groups based on the morphology of the MET were proposed (their comparison with other suprageneric systematics, including molecular systematics, is presented in the table in Chapter 2.3).

Evolutionary interpretations of the presence/absence and the morphology of the metafemoral extensor tendon were radically changed by Ge et al. (2011) who put them into a phylogenetic context and mapped the shapes of the metafemoral extensor tendon on a multigene phylogenetic tree of galerucines and alticines. As mentioned above, the result shows few independent origins of the metafemoral extensor tendon in the alticine-galerucine clade. In addition, there seems to be a correlation between the complexity of the MET and the shape of the metafemur – more swollen and modified metafemur contains usually a highly developed metafemoral extensor tendon. In some lineages of the monophyletic alticine clade, the MET is secondarily reduced to a simpler shape, which demonstrates the possibility of the regression of this character. Some lineages of non-alticine jumping galerucines (*Acrocrypta* group and *Hespera* group) bear a very simple MET without a ventral lobe, other non-alticine jumping galerucines have a simple MET with ventral lobe not exceeding half of MET which is also secondarily present in some true alticine lineages. The ancestral state of the true alticine clade is a well-developed MET with ventral lobe exceeding half of the MET which also evolved in parallel in the *Nonarthra* clade (i.e. the non-alticine jumping galerucine clade). Ge et al. (2011) agree with Furth (1983) that the structural specific in morphology of the MET are shared among closely related genera, but refuses his opinion, that this morphology can be used for higher suprageneric systematics. The high amount of parallelism and homoplasy in MET morphology, i.e. the character originally considered as crucial for highler-lever systematics is discussed by Ge et al. (2011) as one of main reasons of why the former systematics of flea beetles was so obsolete and full of systematic confusions and mistakes. The jumping ability as a character, however, is extremely important and can be considered as one of the major phenomena responsible for the mega-radiation of alticines. Ge et al. (2011) also discuss the advantages of the jumping ability. In their opinion, the jumping could be an evolutionary reaction on appearance of root-feeding larvae in most saltative galerucine lineages. Chrysomelinae, the sister group of Galerucinae s. lat., have usually leaf-feeding larvae. In this situation, larvae and adults can use mutual chemical defence strategies. Alticine larvae do not occupy the same ecological niche with the adults and jumping is a very efficient new strategy, when no larval defence-helpers are found in the area where the adult is present. The small body size of alticines can be also a result of the jumping ability – it might make the jumping escape strategy more efficient physically.

3.3. Karyotype evolution

Karyotypes and cytotaxonomy of flea beetles has been vastly studied during the last two decades of the 20th century, but a problem of these studies is a relative naivity of the author's view on evolution and phylogeny of flea beetles. No phylogenetic information or mapping of characters on phylogenetic trees is used. Meioformulas seem to be very variable in Alticinae and even species in one genus have sometimes distinct differences in chromosome numbers, e. g. in case of *Longitarsus*, where the chromosome number varies from $2n = 26$ to $2n = 32$ (Segarra & Petitpierre 1988). The sex determination in flea beetles is usually the *Drosophila*-type XY, with several modifications, as increasing the number of sex chromosomes X, Y or both, or switch to XO type (Petitpierre et al. 1993; Segarra & Petitpierre 1982; Petitpierre 2006).

A mass of work was done in the cytotaxonomy and karyotype evolution in Oedionychina, particularly in the Neotropics. Cytotaxonomical characters seem to support the monophyly of this group – the majority of Oedionychina has $2n=22$ and the $10+X+y$ meioformula (Virkki & Santiago-Blay 1993). Interestingly, some oedionychines – some *Asphaera* and some *Aspicela* – a big Y chromosome is present in the karyotype, and multiple small X chromosomes. Big Y chromosomes are generally a typical character for oedionychines (Virkki & Santiago-Blay 1993; Petitpierre 2006). The paper is examining also other fissions and fusions of chromosomes in Neotropical Oedionychina. Further study (Petitpierre 2006) show that the 10+X+y meioformula is typical only for Neotropical Oedionychina – Palearctic species show meioformulas 2n=16, 8+X+Y. Petitpierre (2006) suggests that this phenomenon is possibly a result of two centric fusions in autosomes of a possible 2n=22 ancestor. However, in modern phylogeny (Ge et al. 2012), Palearctic *Oedionychis* appears to be a sister group of all Neotropic oedionychines.

Species can be usually separated by examining karyotypes in Alticini, however, meioformulas appear to be conservative between close species, sometimes also intragenerically. Closely related species with the same meioformulas can be usually separated by comparing the size of the chromosomes and the position of the centromere. An interesting situation appears in the genus *Hermaeophaga*, where an intrageneric increase in the number of X chromosomes is known – *H. ruficollis* has 7+Xy, instead of *H. cicatrix* with 7+X_1+X_2+Y (Petitpierre 2006). Despite the usual chromosomal numbers of alticines, which are not extremely small, some genera show artificially small chromosomal numbers – *Homoschema* (2+neoXY) or *Heikertingerella* (4+neoXY), both collected in the West Indies islands. The genus *Heikertingerella* is also special because of a big intrageneric variability in meioformulas (Virkki & Santiago-Blay 1996) – continental species have bigger chromosome numbers. The authors suggest a possibility of an impact of the island evolution (small, isolated population) on the chromosomal number, and compare the case of these two island species with the case of Strepsiptera, where chromosomal numbers are also very low (Ferreira et al. 1984). They suggest the parasitism of Strepsiptera as a similar evolutionary case to island isolation. As mentioned above, some large genera of flea beetles are polymorphic in meioformulas. Sometimes close species groups, which appear to be monophyletic, share the meioformula. This appears in some species groups of *Longitarsus*, e. g. in the case of the species group *L. tabidus* (Fabricius, 1775), where two examined members, *L. tabidus* and *L. australis* (Mulsant et Rey, 1874) share the same karyotype (Petitpierre 2006). However, another closely related species, as *L. nigrofasciatus* (Goeze, 1777), does not share the same karyotype. In some other closely related species, e.g. in *L. pellucidus* (Foudras, 1859), *L. succineus* (Foudras, 1860), *L. codinai* Madar et Madar, 1965 and *L. ochroleucus* (Marsham, 1802), is the karyotype stable and shared (Segarra & Petitpierre 1988). About 40 % of known species has 2n = 20, and because of their morphological and ecological heterogeneity, it is possible to assume this chromosome number as ancestral in *Longitarsus*. The karyotype diversity does not correlate with the specialization on various food plants (Segarra & Petitpierre 1988). A good correlation between karyotype diversity and morphological species-group taxonomy, but also host plant relationships, is present in the case of *Psylliodes*, another widespread megadiverse genus. Also here, a diversity of chromosome number is huge, but the majority of species share 2n=34 (Segarra & Petitpierre 1989).

Karyotypes, meioformulas and sex determination types could be probably be a good character correlated with monophyly of some species groups or genera. However, it probably is not a rich source for finding apomorphies on suprageneric level (Petitpierre 1997).

3.4. Host plant relationships and its evolutionary aspects

Flea beetles, are ancestrally specialized on eudicots and larvae of first alticines were probably root feeders (Ge et al. 2011). Host switches between host families, also to monocots, are very usual, even on intrageneric level, as in the case of the genus *Chaetocnema*, where many species are feeding on various graminoids, (Juncaceae, Cyperaceae, Poaceae), while other feed on Chenopodiaceae, Convolvulaceae or Polygonaceae (Konstantinov et al. 2011). Unfortunately, there is no phylogeny of the genus, so potential multiple switches between monocots and dicots and switches between various host plant families are unknown. This is the case of all flea beetle genera. There are some contributions to the knowledge of host switches in the evolution of other leaf beetles, e. g. reed beetles (Donaciinae), where a phylogeny was done and host plant characters were mapped (Kölsch & Pedersen 2008). In this non-alticine casual situation, we see various interesting switches between host families and their evolutionary implications. It rejects the usual opinion that a close specialization to some host is an “evolutionary trap” which doesn’t allow any further re-generalization or a complete life history change. The phylogeny shows a clade of very closely specialized beetles, where one lineage (the genus *Macroplea*) completely changes its host selection and life history and becomes fully aquatic. The reed beetle case shows us a plenty of possibilities for further research also in many flea beetle groups. In megadiverse genera of flea beetles with wide host specialization diversity (e. g. *Chaetocnema, Longitarsus, Psylliodes* or *Mantura*), we can expect many interesting evolutionary events, as seen in the reed beetle case.

Becerra & Venable (1999) analyzed host plant relationships in the genus *Blepharida* in Mexico in a more evolutionary way – they tried to consider if phylogenetic relationship, chemical defence similarity or biogeographic co-distribution is the major factor explaining host shifts in *Blepharida*. They used a molecular phylogeny of *Blepharida* (which is, unfortunately, a little naive in today’s perspective) and compared it with the phylogeny of *Bursera*, the host plant genus, and with chemical diversity and distributional patterns of the host species. The analysis showed chemical similarity as the major phenomenon which allows a monophagous species of *Blepharida* to change the host, instead of situations, when more species of *Bursera* occur directly on the same locality, but *Blepharida* feeds and develop only on species with the same chemical defence strategy. One exception, *B. alternata*, however, appeared to be polyphagous and feed on many species of *Bursera* with different chemical defence strategies, which occur in its distributional range.

Some alticines also switched their host range from angiosperms to ferns (e. g. *Schenklingia*) or equisetophytes (*Hippuriphila*) (Kimoto 2000; Konstantinov & Vandenberg 1996). a surprisingly big generic diversity was also found in association with moss (this strategy is discussed in the Chapter 3.5). Bark or wood feeding is not known among Alticini.

The way of larval interactions with host plants is also diverse among flea beetles. Usually, larvae of flea beetles are root feeders, some groups, (e. g. *Altica* group or *Blepharida* group) have externally leaf feeding larvae (Konstantinov & Vandenberg 1996; Hua et al. 2014), and some other flea beetles (e. g. *Dibolia, Podagricomela, Sphaeroderma,* some *Phyllotreta*) have leaf-mining larvae (Santiago-Blay 2004; Hua et al. 2015). Adults feed usually on leaves, some species on flowers. An example are adults of *Luperomorpha xanthodera,* an Oriental species which was introduced to Europe with flowering garden plants and become invasive (Del Bene & Conti 2009). However, anthophagy is more common among flea beetles and is known e. g. in the genus *Neocrepidodera* or *Altica* (Bieńkowski 2010). *Nonarthra* and *Arsipoda* were documented to be pollen feeders (Samuelson 1989).

The majority of flea beetles are oligophagous specialists. However, some species are monophagous and other are widely polyphagous. An interesting contribution of to biology of polyphagous alticines is a study on *Phyllotreta nemorum* and its colonization a new food plant (*Barbarea vulgaris*) in Denmark (de Jong & Nielsen 1999). The probability of the success in feeding on the new food plant between individuals of *P. nemorum* is dependant on the genotype.

While feeding on host plants, some flea beetles had to involve ways how to overcome different ways of plant chemical defence. Those defence strategies, however, stimulate evolution in some flea beetle genera, because of lower competition on toxic plants. This is the case of the genus *Phyllotreta,* where species are specialized usually on Brassicaceae and related families Capparaceae and Resedaceae. Crucifers contain mustard oil glucosides, which makes them unexploitable for the majority of beetles. However, *Phyllotreta* involved biochemical strategies to overcome this problem and even uses glucosides as a chemical marker for finding their host plants (Furth 1979).

An outstanding phenomenon, related to host plant toxicity, is chemical defence and toxicity of flea beetles themselves. Free-living larvae of the *Blepharida* group are able to use plant toxins from their host in their chemical defence, while they cover their body into a fecal coat and present the plant toxin in their feces (Prathapan & Chaboo 2011). The predation avoidance has two sides – the fecal coat is toxic and it also can work as a mimetic element. The strategy was firstly documented in the case of *Blepharida rhois*, where chemicals from the host plant *Rhus glabra* are used as a repellents and defensives in the fecal shield for avoiding ant attacs. When fed with a non-poisonous plant (e. g. lettuce), the fecal coat is not effective in defence against ants (Vencl & Morton 1998). In the *Blepharida* group, some species are also able to synthetize their own toxins. An interesting case of flea beetle toxicity is documented in Africa, where some poisonous species of the genera *Diamphidia*, *Polyclada* and *Blepharida* are used by indigenous Khoisan people for preparing arrow poisons. In the best-studied case of the genus *Diamphidia*, all developmental stages (larva, pupa, adult) are poisonous and pupae are used for extracting arrow poison (Woollard et al. 1984; Chaboo et al. 2016). The poison, diamphotoxin, is a protein (Mebs et al. 1982). Another, obscure case of toxicity was documented in larvae and adults of *Altica aenea* in Brisbane, Australia. When individuals feeding on a emerged host plant *Ludwigia* swam in water around, they killed mosquito larvae probably by releasing their defense secrets. The description seems that larvae were swimming in the water randomly, although they are not aquatic (Hamlyn-Harris 1930; Reid & Beatson 2015).

3.5. Specific life strategies: terrestrial and moss inhabitance

One of the very obscure habitats flea beetles inhabit is leaf litter, plant detritus and, especially, moss cushions. There are about 15 various genera of moss inhabiting flea beetles known up to date (Konstantinov et al. 2013), and numerous other terrestrial or semi-terrestrial species. In Czech fauna, the terrestrial life style is present for example in the genus *Orestia* Chevrolat, 1836. The genus occurs in subalpine and montane forests in mountain ranges across the Palaearctic, and is usually found by sifting plant detritus and leaf litter along stream edges (Čížek & Doguet 2008). Some species of the genus *Neocrepidodera* are also terrestrial, wingless, inhabiting the alpine and nival zone of European mountains. Mountain ranges in other parts of the world also host specific alpine apterous flea beetles: for examplethe genus *Sjoestedtinia* Weise, 1910 inhabits alpine zone of East African volcanoes of the Kilimanjaro mountain range – Mt. Kenya and Mt. Kilimanjaro (Biondi & D’Alessandro 2010).

Moss-inhabiting flea beetles are generally poorly known, because their habitats are largely omitted by the majority of leaf beetle researchers. Moreover, the ranges of moss-inhabiting species are usually rather limited, and majority of species found in moss cushions in previously unexplored sites outside the western Palearctic are undescribed (Konstantinov et al. 2013). The majority of known moss-inhabiting flea beetle species has been described during last years and it is likely that the majority of the species richness is still unknown. They are however known from all biogeographic regions already (Konstantinov & Lourdes Chamorro-Lacayo 2006; Konstantinov et al. 2013; Konstantinov & Konstantinova 2011).

The systematic and phylogenetic position of moss inhabiting flea beetle genera remains unclear. It is likely that the association with moss evolved multiple times independently, which is indicated by the morphology and distribution:_the moss-inhabiting genera differ from each other by characters usually constant within genus-groups (i.e. the morphology of anterior coxal cavities), and they are present world-wide, despite their very low dispersal abilities once associated with moss and leaf litter habitats.

Convergence of morphological characters is nevertheless outstanding in some cases. For example, the moss-inhabiting genera *Clavicornaltica* Scherer, 1974 from the Orienal and Australian Regions, and

Kiskeya Konstantinov & Chamorro-Lacayo, 2006 endemic to the West Indies share many unusual morphological characters including extremely small body (usually less than 1 mm), compactly rounded and very convex body shape, and last antennomeres significantly broadened and forming an apical antennal club (Konstantinov & Lourdes Chamorro-Lacayo 2006). Despite these similarities, they are likely not closely related: *Kiskeya* is a member of the subtribe Monoplatina distributed in Neotropical and Australian Regions only, whereas *Clavicornaltica* is considered closely related to Oriental moss-inhabiting and terrestrial genera *Kamala* or *Ivalia* (Scherer 1974).

Larvae of moss inhabiting flea beetles are not well known and only those of Old World genera *Mniophila* Stephens, 1831and *Ivalia* Jacoby, 1887 are described at the moment (Cox 1997; Duckett et al. 2006). However, studies on larval morphology of Neotropical monoplatine genera are in preparation (Konstantinov, pers. comm. 2016).

Suprisingly, the diet of moss-living alticines is not known in the majority of genera, and bryophagy in adults was confirmed only in the western Palearctic genus *Mniophila* (Nadein 2009) and the Asian species *Cangshanaltica nigra*, in which microscopical fragments of *Hypnum* moss were found after dissecting the gut (Konstantinov et al. 2013). Konstantinov et al. (2013) also mention the observation of bryophagy in some undescribed species of *Ivalia* by the Indian specialist K. D. Prathapan.

Biogeography of moss-inhabiting flea beetles is very interesting and would deserve further studies. The beetles have low dispersal abilities, as they are unable to fly; however they oftenform many endemic species on islands, eventually in mountain ranges, which are in fact also island-like geographical structures. This is the case of the Neotropical genus *Kiskeya*, which is distributed in Puerto Rico and Dominican Republic only. There are also other wingless and moss-inhabiting genera with Carribean distribution, as *Distigmoptera* or *Apleuraltica* (Konstantinov and Konstantinova 2011; Konstantinov and Lourdes Chamorro-Lacayo 2006). In Asia, the island phenomenon is not known for oceanic islands, but for isolated mountain ranges. This is the case of the genus *Benedictus* distributed in the whole Himalayan area from Pakistan and India to China and Thailand. Usually, particular species of *Benedictus* are locally endemic for small regions across Himalaya (Sprecher-Uebersax et al. 2008). Similar, but not well studied case could be the newly described genus *Cangshanaltica*, which was found in the Cangshan mountain range in China and, suprisingly, in the range of Doi Inthanon in Thailand. Because this genus is also wingless, we can expect discoveries of additional species in mountains between and around known localities (Damaška & Konstantinov 2016; Konstantinov et al. 2013).

We can formulate several alternative hypotheses about the origin of the discontinuous ranges of the moss-inhabiting species:

(1) Dispersal of a winged ancestor of extant wingless species, or passive dispersal of a wingless ancestor. In case of this scenario, the phylogeny would reveal a starting point of this dispersal. If more than one species are distributed on one island (what is for example the case of *Kiskeya*), also the dispersal direction could be visible in the phylogeny. If all species of one island form a paraphylum including species from another island, dispersal from the point of origin through another island would be demonstrated.

(2) Vicariance after a geological event, e. g. the break-up of the island from the continent . In this case, the time of divergence of the island lineage would correspond to the (sub)division of the island, and the topology would follow particular landmass splitting events.

(3) Vicariance after some climatic event, e. g. end of the last glaciation. This may be the case of montane species inhabiting colder forest habitats which were more widespread during colder periods. After warming, these forests migrated to higher altitudes and their ranges became discontinuous, which was the starting event for flea beetle speciation. The same case (i.e. splitting of originally continuous range of the flea beetle) would appear on islands which were parts of a landmass during the last glaciation, when the sea surface was lower. We would see then a few species groups (respecting hypothetical more ancestor species) with many species lineages being equally old. Possibly, this scenario seems to be represented by the case of *Montiaphthona* Scherer, 1961 in East African montane forests. A widespread population of one species of *Montiaphtnona* has been likely isolated in montane forests, when the temperatures became higher and the cool forest ecosystem was pushed into some isolated mountains (Scherer 1988).

Despite there are no studies directly focused on dispersal abilities of moss-inhabiting flea beetles, we can theoretize about their migration by using other studies. Flø & Hågvar (2013) report abilities of non-winged small invertebrates (e. g. springtails) of passive dispersal by wind together with small pieces of moss and soil in Fennoscandia. Furth (1979) suggests that flea beetles could be able to survive passive aerial migration in higher layers of the athmosphere and that this ability may be a crucial phenomenon for migration of flea beetles in desert areas of the Middle East, where strong seasonal winds are present. Moss-inhabiting flea beetles ale known to inhabit also epiphytic mosses on trunks and branches of trees in cloud forests in high elevations (Damaška & Konstantinov 2016). Slopes of mountains are often exposed to very strong winds, especially in typhoon, monsoon or hurricane areas, where majority of moss-inhabiting flea beetles are living (Himalayas, Southeast Asia and the Carribean). The jumping ability of moss-inhabiting flea beetles allows them to jump off when disturbed. Therefore, I am suggesting a scenario of how migration of montane moss-inhabiting flea beetles could be possible – they may be catught by strong winds from tree branches and become passive aerial migrants. This ability could be stronger in case of flea beetles than in cases of other moss-inhabiting beetles, because of their jumping ability – the disturbance caused by the strong branch movement in the wind could easily make them jump and get caught by the wind.

At the moment, there is no information about the age of species divergences within moss-inahabiting genera, preventing the formulation of more accurate hypotheses. A possibly "good" case of vicariance is represented by Caucasian and Crimean species of the genus *Mniophila*. Four different species are distributed in the Black Sea region – *Mniophila caucasica* Nadein, 2009 is widespread in the Caucasus, *Mniophila transcaucasica* Nadein, 2009 is known from one locality in Armenia, *Mniophila turcica* Medvedev, 1970 lives around Rize in northern Turkey and *Mniophila taurica* Nadein, 2009 is endemic for Crimea. Another two species, *Mniophila muscorum* (Koch, 1803) and *Mniophila bosnica* Apfelbeck, 1914 are widespread in Europe (Nadein 2009). The historical scenario of European *Mniophila* is enigmatic, because distributional ranges of these two species overlap. A possible scenario is vicariance after isolation of ancestor *Mniophila* populations *Mniophila* in two different glacial refuges. When forests covered Europe again, both species migrated and their ranges began to overlap.

Very interesting field for further studies of this problem could be the case of the formerly mentioned genus *Clavicornaltica*. In contrast to the majority of moss-inhabiting flea beetles including *Kiskeya*, males of many species of *Clavicornaltica* are able to fly, whereas other species are completely wingless (Scherer 1974). The genus in very widely distributed and hyperdiverse – studies show a high level of endemism and a high local diversity– one locality may be inhabited by multiple endemic species (Medvedev 1996; Konstantinov & Duckett 2005). Moreover, some species (e. g. *C. dali*) are completely wingless (Konstantinov & Duckett 2005).

4. Biogeography

4.1. Recent distribution

Flea beetles are distributed worldwide except in the Antarctica (Konstantinov and Vandenberg 1996), and are also absent from some isolated islands (e. g. Hawaii) (Sekerka, pers comm). The Neotropical region has the most diverse fauna (around 240 genera), followed by the Oriental region (around 180 genera), Afrotropical region (around 100 genera), Palearctic region (around 60 genera), and the lowest diversity is known from Australia and Oceania (around 50 genera) and the Nearctic region (around 40 genera) (Konstantinov & Vandenberg 1996; Biondi & D'Alessandro 2012; Nadein 2013; Scherer 1988). A review of the biogeographic knowledge of Alticini and suggesting some hypotheses on their origin was presented by Scherer (1988). In this text, I will follow this work, commenting its information by new contributions to the problem.

(1) **Neotropical** fauna is the most diverse at generic level, and the majority of the genera is endemic to the mainland of South America. Cosmopolitan genera (e. g. *Longitarsus, Epitrix* and *Chaetocnema*) are also distributed in the Neotropics, but their presence in the South America is considered a result of the Great American Interchange by Scherer (1988). This hypothesis is corroborated by their distributional pattern in South America – the number of species in these genera decreases rapidly from north to south. It is difficult to test if this phenomenon is really an effect of a migration from the north, or simply a non-diversification or prior extinction caused by hostile and arid conditions of Patagonia and former glaciation. Especially, the case of the genus *Epitrix* could be very intriguing, because there is a diversity center of this genus in Central and South Americas (Deczynski 2014; Konstantinov & Vandenberg 1996). Fauna of the Neotropics is also typical by presence of two faunal radiations: the subtribes Monoplatini and Oedionychini. While the subtribe Oedionychini is distributed worldwide with a huge Neotropical monophyletic radiation (Ge et al. 2012), Monoplatini are, with one spectacular exception in Australia, endemic to Neotropics (Seeno & Wilcox 1982; Scherer 1988). There is no large modern study of Neotropical alticine genera after the work by Scherer (1983), who also mentions tens of genera described additionally, never revised or keyed. Also, some new genera and species of moss-inhabiting flea beetles were described recently (see Chapter 3.5).

(2) **Nearctic** fauna is relatively poor and the majority of North American genera is not endemic – there are many Neotropical and Holarctic faunal elements – likely results of migration events. Examples of genera shared with the Neotropics are e. g. *Systena* or *Kuschelina*. Genera shared with the Palearctic are e. g. *Orestia* or *Derocrepis*. A typically Holarctic genus is *Hippuriphila* (Konstantinov & Vandenberg 1996). There are also many worldwide-distributed genera largely diversified in the Nearctic region, e. g. *Phyllotreta*, *Longitarsus*, *Epitrix* or *Chaetocnema* (Riley et al. 2003; Smith 1985; Deczynski 2014; Furth & Savini 1996; Furth 1985).

(3) **Palearctic** fauna is slightly more diversified at generic level than the Nearctic one; however, the delimitation of the “true Palearctic fauna” is very difficult due to the unclear delimitation of the Palearctic region in Eastern Asia and penetration of the Oriental fauna to the north. The genus *Nonarthra* is an example: the genus is typically Oriental, but reaches Japan and Siberia (Kimoto 1965; Konstantinov & Vandenberg 1996). Only a few genera are endemic for the Palearctic region, some of them distributed in the mountains or in the moss (*Mniophila, Apteropeda*), other are probably faunal relicts (e. g. *Oedionychis*, *Arrhenocoela*). The distribution of Oedionychina in the Palearctic region is very interesting, because only two species are present (both on the Atlantic coast of Morocco and the Iberian Penninsula) and these two species are not closely related to any of the widespread Oriental or Afrotropic genera; they form a sister group of the monophyletic Neotropical Oedionychina clade (Ge et al. 2012). There is also a study on biogeography of the Macaronesian islands, which shows the fauna of Madeira and Canary islands Palearctic, unlike the fauna of Cape Verde, which is Afrotropical (Biondi 1990).

(4) **Oriental** fauna is very rich. This region is geographically very complex – it is formed by the Indian subcontinent (having around 60 endemic alticine genera), the Indochina, and the Sundaland, where many genera and species are diversified on islands and the diversity is vastly understudied (Scherer 1988; Kimoto 2000). Many of the Oriental alticine genera are also present in the southern Palearctic, especially in southern China, where the border between Palearctic and Oriental regions is unclear (Döberl 2010). A study on the faunal composition of chrysomelid beetles in the Wallacea (i.e. the transitional region between the Oriental and Australasian regions, represented by the Lesser Sunda archipelago, the Maluku islands and the island of Celebes) was performed by Mohamedsaid (2009). He assumes that 41% of the Lesser Sunda leaf beetle fauna is derived from the Oriental region; while 46% of the Chrysomelidae fauna is endemic (numbers are on the species level). Only 3% are derived from the Australasian region. Interestingly, the Wallace's line appears to be a strong migration barrier for Galerucinae *s. str.*

(5) **Australian** region has the lowest number of alticine species, but many endemic genera are present (e. g. *Platycepha, Bellaltica, Pedethma* etc.). Also fauna of oceanic islands adjacent to mainland Australia is interesting by the presence of some endemic genera (e. g. *Alema* or *Pleuraltica* endemic to New Zealand and, in the case of the second genus, also Norfolk Island) (Scherer 1973; Reid 1988). Also, some typically Australian genera, as *Licyllus* or *Arsipoda* also have few species in the Oriental region (Mohamedsaid 2016; Scherer 1973). Corresponding to other animal groups, there are some genera of Alticini which are distributed worldwide, but absent in Australia. This is for example the case of *Dibolia* (no species in Australia), and *Phyllotreta* (one species in Australia) (Nadein 2013; Scherer 1973). The fauna of the Oceania has mainly an Oriental origin. The alticine fauna of Papua-New Guinea is vastly understudied. Only a few contributions were made, usually describing new genera (Samuelson 1971; Samuelson 1965; Samuelson 1969; Medvedev 2010), so we can expect large amount of new taxa to be described from this area. Endemic genera known from New Guinea are represented e. g. by *Setsaltica* or *Maaltica*. An interesting member of the Australian fauna is the genus *Opistopygme* which belongs to the mainly South American subtribe Monoplatina, but has also some characters typical for non-monoplatine Australian genera (Scherer 1988).

(6) **Afrotropical** region is the poorest big tropical continent in alticine fauna. However, the biogeography of the flea beetle fauna was very vastly studied, unlike in other zoogeographic regions. The delimitation between Palearctic and Afrotropical regions is very disputable and sometimes, the Saharan desert is assumed as a part of the Afrotropical region (Kreft & Jetz 2010). The same situation appears on the Arabian Peninsula. Medvedev (1997) comments the faunal composition of whole Chrysomelidae of the Arabian Peninsula and assumes Yemen to be Afrotropical (with 71 % of the leaf beetle fauna of Afrotropical origin), unlike northern Oman having only 22 % of the fauna of Afrotropical origin and 78% of Palearctic origin. The whole Arabian Peninsula has 39 % of the Chrysomelidae fauna of Afrotropical origin. The influence of the Oriental fauna is very low – 3%. The

only endemic leaf beetle genus in the area is a flea beetle genus *Yemenaltica*, which is considered to be related to Afrotropical genera. Interestingly, in the fauna of Palearctic origin, the influence of the Irano-Turanian area is lower than the influence of the Mediterranean and North African desert areas. The whole Afrotropical region can be distinctly divided into a Malgasy and continental areas according to the flea beetle fauna; based on a cluster analysis, Mascarenes and Seychelles show relation to other biogeographic regions and their flea beetle fauna is not coherent with the fauna of Africa and Madagascar (Biondi & D'Alessandro 2012). A high percentage (71 %) of Afrotropical flea beetle genera are endemic, the highest percentage of shared genera is with Oriental and Palearctic regions. An interesting member of the Afrotropical fauna is the genus *Zomba*, which is the only Afrotropical member of Monoplatina, and, together with Australian *Opistopygme*, the only non-Neotropical monoplatine. a possibility of a relictual Gondwanan origin is discussed (Biondi & D'Alessandro 2012). Some biogeographic analyses were done to contribute the understanding of Afrotropical fauna and its distributional patterns (Biondi 2006; Biondi et al. 2015). Different 'chorotypes' of distribution were recognized in the fauna of Afrotropical *Chaetocnema* and some endemism zones (e. g. in Western Cape or Madagascar) were described. Species of *Chaetocnema* have usually regionally restricted ranges, only a few species are widespread. The endemism of *Chaetocnema* in Madagascar is assumed to be 'higher than that recorded for birds' (Biondi et al. 2015). Unsurprisingly, species with wide ecological valence are usually widespread, unlike biotope specialists. **Madagascar** has 13 of total 39 genera of flea beetles endemic (e. g. *Neodera, Ntaolaltica* or *Anaxerta*). Some of them, as *Ntaolaltica* or *Antanemora* are considered to be related to some Oriental genera (including the genus *Chabria*, which is distributed both in the Oriental and Afrotropical regions), another, as *Pseudophygasia* or *Neodera*, show more relations to native African fauna (Biondi & D'Alessandro 2013).

4.2. Understanding flea beetle biogeography

With information about time of origin of Galerucinae and with partial knowledge of flea beetle phylogeny, it should be possible to provide some interpretations of the historical biogeography of some groups. At the generic level, we can see a complete confusion when trying to map biogeography on the tree by Ge et al. (2012) (biogeographic data adopted from Nadein (2013) and Seeno & Wilcox (1982)) – mapped distribution is presented in Fig 6. The problem is in the sampling bias – the sampling used in the analysis by Ge et al. (2012) is strongly biased towards Oriental fauna , and other, especially Neotropical, Afrotropical and Australian genera are absent or underrepresented. Despite of that, some interesting information can be revealed from the tree. In the case of the Oedionychina, we see two independent lineages in North America. This shows the formerly mentioned fact that many different lineages of Neotropical Oedionychina migrated to the Nearctic region relatively recently, probably during the Great American Interchange (Pliocene). The situation of the cosmopolitan genera (e. g. *Longitarsus, Chaetocnema* or *Psylliodes*) in the Neotropics is very complex and the mapping cannot yield any satisfactory explanation, because the genera are old and diverse. Thus, we need complex (and dated) phylogenies of these genera for resolving their migration pathways. Some work was published on biogeography of the cosmopolitan genera in other regions. Biondi (2001) tried to reconstruct migration routes staying behind the faunal composition of *Chaetocnema* in Madagascar. He assumes two endemic species descending from the Oriental (Eurasian) ancestors (and tries to hypothesize possible closely related Oriental genera, which seems somewhat foolish because Oriental *Chaetocnema* is totally understudied), other Madagascar endemics are considered to be of African origin. Two possible radiations on Madagascar are described, each with few species, other endemics in Madagascar are assumed to be single descendants of independent migrations. If true, this situation just verifies biogeographic notes considering Madagascar as an isolated 'little continent' more than a big island. However, these studies are very problematic, because the lack of the phylogenetic knowledge. Modern casual studies show us, that biogeographic studies without knowledge about phylogeny can show us interesting patterns of today's organism distribution, which can lead to several ecologic theories, but are not able to clarify historically biogeographic scenarios, which led to recent distributional ranges (Balke et al. 2009). Therefore, it is necessary to wait for complex phylogenetic analyses.

Some cases, when closely related taxa have disjunctive ranges, are possibly explainable as relicts of some ancient widespread taxa, the majority of which became extinct and some lineages became isolated in completely different parts of the world. This can possibly be the case of formerly mentioned genera *Psylliodes, Psyllototus* and *Chamealtica*. *Psyllototus*, a fossil genus from Baltic amber, is considered to be closely related with *Psylliodes* differing only in having 11 antennomeres (as plesiomorphic among Alticini) instead of 10 (an apomorphy of *Psylliodes*). *Chamealtica* also appears to be very closely related to *Psyllototus*, but occurs only in Chile, unlike the Baltic fossil *Psyllototus* and cosmopolitan *Psylliodes*. As *Psylliodes* in recent times, *Psyllototus* could also be a very successful, diverse and widespread genus. In one lineage of *Psyllototus*, an evolutionary event occurred by losing one antennomere – this hypothetical lineage would be the stem lineage of recent *Psylliodes* radiation. During the Neogene, *Psyllototus* became extinct on a majority of its distributional range and was replaced by other lineages, which became widespread. One of these newly successful lineages was also the *Psylliodes* lineage, which became monophyletic after extinction of majority of *Psyllototus*. However, another lineage of the *Psyllototus* radiation survived the extinction isolated in Chile and become extant *Chamealtica*. This scenario is possibly applicable for many other disjunctive ranges of taxa. In mammals, such scenarios are known e. g. in the case of camels (reference), however, in insects, searching for residua of ancient widespread ranges seems to be a novel way of studies of insect distribution. a similar phenomenon is suggested by Scherer (1988) in the case of the genus *Terpnochlorus*, which is distributed in Africa, Madagascar and South America. An interesting situation of a biogeographic disjunction is represented by *Longitarsus capensis* and *L. anchusae* species groups, which are assumed to be very closely related (without proper phylogenetic analyses, only based on the morphotaxonomic view), but the *L. capensis* group is endemic in the Mediterranean biome area of the Cape floral region in South Africa (Biondi & D'Alessandro 2008) and *L. anchusae*. A possible origin of the disjunction is considered to be a migration event after Miocene, when the fynbos vegetation arose in the Western Cape. The migration routes had to be some arid belts in Africa. However, more hypotheses, not formulated in the paper, are possible – for example those discussed below. And, again – we need a proper phylogenetic analysis to bring more insight into the relationships in the genus. The morphological similarity could be a plesiomorphy and the "*anchusae* – *capensis*" group could be paraphyletic with many morphologically different species complexes in Africa. In this situation, the explanation of the similarity would be very simple.

Interesting cases in flea beetle biology are also possible island radiations. However, these studies still lack the insight by modern molecular phylogenetic methods. For example, a casual study was provided by D'Alessandro et al. (2016) about the genus *Arsipoda* in New Caledonia. This island is well-known as enigmatic in biogeography, because it has many relictual Gondwanan elements in other taxa, especially in plants. The taxonomic work of the mentioned study is on a very good level, but the phylogeny provided is only morphological and using obsolete phylogenetic methods. Even the sampling of outgroups is inaccurate (only two non-Caledonian species were used), so the phylogenetic results may be largely biased. However, there is a very interesting study on New Caledonia done on another leaf beetle group – Eumolpinae, which is very diverse in New Caledonia Papadopoulou et al. (2013). We also cannot consider that all of the New Caledonian eumolpines are a monophyletic group, but we can see the divergences between eumolpine lineages from the New Caledonia much younger than possible for considering some parts of the fauna as a Gondwanan relict. Fauna of the Eumolpinae in New Caledonia is a result of a few (or, strikingly, only one) migration events and further adaptive radiations. Another case of a radiation on islands (now in flea beetles again) is the case of the Madagascar endemic genus *Neodera*, which is studied by D'Alessandro et al. (2014). The genus shows a big tendency to microendemism in Madagascar and is associated with primary humid forests. These forests are very endangered in Madagascar due to the massive deforestation and *Neodera* is usually unable to survive in secondary forests, so it can be considered as an ecological indicator and also an endangered genus. The diversification of *Neodera* in Madagascar seems to be a result of an evolution in some centers of endemism (especially mountain ranges with humid forests, which refuged forest species during the more arid times and also led them to diversify). The paper presents many different hypotheses of the diversifications, however, there is only a relatively primitive morphological phylogeny again. An interesting situation appears on the Canary islands. The island of Tenerife seems to be a 'catching island', where invaders from surrounding areas arrive. Then, they can migrate from Tenerife to other islands around, so some Canarian species groups can possibly originate on Tenerife and have the diversity center there – however, phylogenetic data for Alticini are not existing again in this case (Biondi 1990).

Specific aspects of flea beetle biogeography, which cannot be missed, are recent biological invasions of flea beetles. The genus *Epitrix* has many species, which become invasive as crop pests on *Solanaceae*, especially those from North America (Bieńkowski & Orlova-Bienkowskaja 2016). Another case of an invasive alticine is the formerly mentioned species *Luperomorpha xanthodera*, which invaded Europe in containers with ornamental plants (Del Bene & Conti 2009). A comic situation appeared in the case of *Epitrix papa*, described from the Iberian Peninsula as an invasive pest on potatoes, but its native range is not known and it is similar to some Californian species of the genus (Orlova-Bienkowskaja 2015).

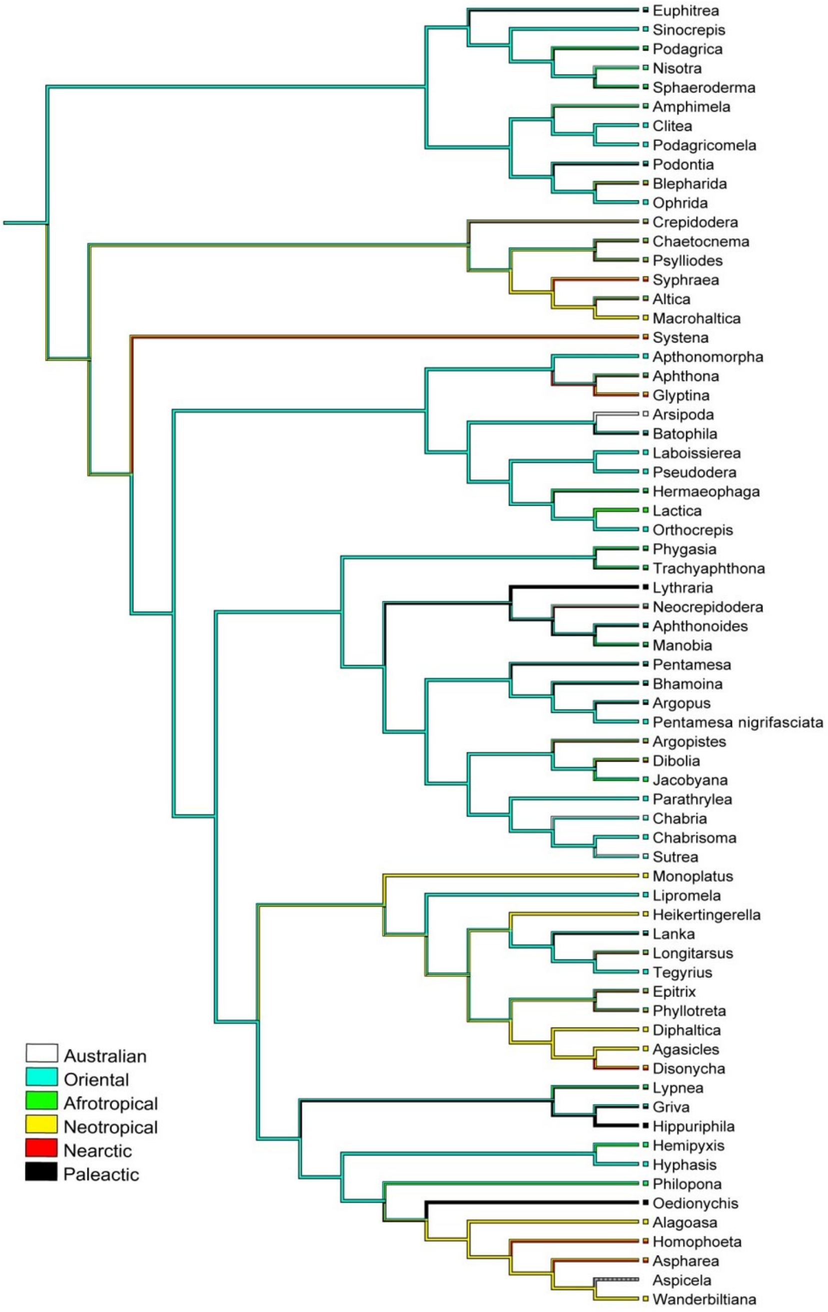

Fig. 6. – Distribution of flea beetles in zoogeographic regions based on the phylogeny by Ge et al. (2012) and data from Nadein (2013), visualized in Mesquite software (Maddison & Maddison 2017).

5. Summary

The systematic position of Alticini and the multiple origin of the jumping ability in various lineages among Galerucinae *s. str.* is an interesting discovery resulting from including molecular data and we can expect more interesting views and insights into alticine biology and evolution by improving the molecular phylogeny by adding more taxa into the sampling and extending the number of used genes. Molecular phylogenies of certain genera, especially those cosmopolitan, megadiverse ones (*Longitarsus, Chaetocnema, Phyllotreta, Aphthona, Epitrix, Psylliodes*) and their proper taxonomic revisions are required for resolving some traits in their evolution and can help to explain their historical biogeography. Better sampling and further molecular phylogenetic studies of moss inhabiting flea beetles can help in explaining their expected multiple origin and parallel evolution. It can bring more light into understanding their enigmatic dispersal abilities and can also be useful for general understanding of the evolution organisms with possibly low dispersal abilities, their evolutionary traits and circumstances of their specialization. Thus, Alticini are a possibly perfect model taxon for studies on insect evolution, historical biogeography and ecological traits. Additionally, the poor knowledge of their diversity is a perfect field for an enthusiastic evolutionary taxonomist, who is interested in travelling all around the world in search for interesting and beautiful unknown organisms, trying to unearth monumental stories of how they got where they are and what they look like – the stories hidden behind all the organisms, in millions of years of their history.

6. References

Balke, M. et al., 2009. New Guinea highland origin of a widespread arthropod supertramp. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1666), pp.2359–2367.

Barth, R., 1954. O Aparelho Saltatório do Halticíneo Homophoeta sexnotata Har. (Coleoptera). *Memórias do Instituto Osvaldo Cruz*, 52(2), pp.365–376.

Becerra, J.X. & Venable, D.L., 1999. Macroevolution of insect-plant associations: the relevance of host biogeography to host affiliation. *Proceedings of the National Academy of Sciences of the United States of America*, 96(22), pp.12626–12631.

Del Bene, G. & Conti, B., 2009. Notes on the biology and ethology of Luperomorpha xanthodera, a flea beetle recently introduced into Europe. *Bulletin of Insectology*, 62(1), pp.61–68.

Bieńkowski, A.O. & Orlova-Bienkowskaja, M.J., 2016. Key to Holarctic species of Epitrix flea beetles (Coleoptera: Chrysomelidae: Galerucinae: Alticini) with review of their distribution, host plants and history of invasions. *Zootaxa*, 4175(5), pp.401–435.

Bieńkowski, a. O., 2010. Anthophagy in the leaf beetles (Coleoptera, Chrysomelidae). *Entomological Review*, 90(4), pp.423–432.

Biondi, M., 2006. Biogeographical analysis of the flea beetle genus Chaetocnema in the Afrotropical Region : distribution patterns and areas of endemism beetle genus Chaetocnema in the Afrotropical Region : distribution patterns and areas of endemism. *Journal of Biogeography*, 33, pp.720–730.

Biondi, M., 1990. Flea beetles and biogeography of the Macaronesia. (Coleoptera, Chrysomelidae, Alticinae). *Conference: International Symposium on "Biogeographical aspects of insularity", At Rome 1987*, 89, pp.521–532.

Biondi, M., 2014. Paolaltica eocenica new genus and new species of flea beetle (Coleoptera: Chrysomelidae: Galerucinae: Alticini) from Baltic amber. *Zootaxa*, 3852(4), pp.496–500.

Biondi, M., 2001. Revision of the species of Chaetocnema from Madagascar (Coleoptera: Chrysomelidae: Alticinae). *European Journal of Entomology*, 98, pp.233–248.

Biondi, M. & D'Alessandro, P., 2012. Afrotropical flea beetle genera: a key to their identification, updated catalogue and biogeographical analysis (Coleoptera, Chrysomelidae, Galerucinae, Alticini). *ZooKeys*, 253, pp.1–158. Available at: http://www.pensoft.net/journals/zookeys/article/3414/abstract/.

Biondi, M. & D'Alessandro, P., 2010. Genus-group names of Afrotropical flea beetles (Coleoptera: Chrysomelidae: Alticinae): Annotated catalogue and biogeographical notes. *European Journal of Entomology*, 107(3), pp.401–424.

Biondi, M. & D'Alessandro, P., 2013. Ntaolaltica and Pseudophygasia, two new flea beetle genera from Madagascar (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Insect Systematics & Evolution*, 44(1), pp.93–106. Available at: http://booksandjournals.brillonline.com/content/journals/10.1163/1876312x-04401004.

Biondi, M. & D'Alessandro, P., 2008. Taxonomical revision of the Longitarsus capensis species-group : An example of Mediterranean-southern African disjunct distributions (Coleoptera : Chrysomelidae). *European Journal of Entomology*, 105, pp.719–736.

Biondi, M. & De Nardis, G., 2002. Natural history of the flea beetle genus Arrhenocoela Foudras (Coleoptera, Chrysomelidae, Alticinae). *Italian Journal of Zoology*, 69(August), pp.83–93.

Biondi, M., Urbani, F. & D'Alessandro, P., 2015. Relationships between the geographic distribution of phytophagous insects and different types of vegetation: A case study of the flea beetle genus Chaetocnema (Coleoptera: Chrysomelidae) in the Afrotropical region. *European Journal of Entomology*, 112(2), pp.311–327. Available at: http://www.scopus.com/inward/record.url?eid=2-s2.0-84928892156&partnerID=tZOtx3y1.

Biondi, M., Urbani, F. & D'Alessandro, P., 2013. Revision of the Aphthona cookei species group in Sub-Saharan Africa: pests of Jatropha curcas L. in biodiesel plantations (Coleoptera, Chrysomelidae, Galerucinae, Alticini). *Entomologia*, 1(1), p.7. Available at: http://sei.pagepress.org/index.php/entomologia/article/view/entomologia.2013.e7.

Bouchard, P. et al., 2011. Family-group names in Coleoptera (Insecta). *ZooKeys*, 88(SPEC. ISSUE), pp.1–972.

Brackenbury, J. & Wang, R., 1995. Ballistics and visual targeting in flea-beetles (Alticinae). *The*

Journal of Experimental Bbiology, 198, pp.1931–1942. Available at: http://www.ncbi.nlm.nih.gov/pubmed/9319842.

Buckland, P.I. & Buckland, P.C., 2012. Species found as fossils in Quaternary sediments. In A. G. Duff, ed. *Checklist of Bettles of the British Isles*. Pemberley Books, pp. 127–130.

Bukejs, A., 2015. First fossil Lamprosomatinae leaf beetles (Coleoptera : Chrysomelidae) with descriptions of new genera and species from Baltic amber. *Zootaxa*, 3931(1), pp.127–139.

Bukejs, A., Biondi, M. & Alekseev, V.I., 2016. New records and species of Crepidodera Chevrolat (Coleoptera: Chrysomelidae) in Eocene European amber, with a brief review of described fossil beetles from Bitterfeld amber. *Zootaxa*, 4193(2), pp.390–400.

Bukejs, A., Biondi, M. & Alekseev, V.I., 2015. Sucinolivolia torpida—a new genus and species of flea-beetles (Coleoptera: Chrysomelidae: Galerucinae) from Baltic amber. *Zootaxa*, 4058(1), p.5326.

Bukejs, A. & Nadein, K.S., 2013. A second species of Psyllototus (Coleoptera: Chrysomelidae: Galerucinae: Alticini) from the Upper Eocene Baltic amber. *Zootaxa*, 3609(5).

Bünnige, M., Hilker, M. & Dobler, S., 2008. Convergent evolution of chemical defence in Galerucine larvae. *Biological Journal of the Linnean Society*, 93(1), pp.165–175.

Burrows, M., Shaw, S.R. & Sutton, G.P., 2008. Resilin and chitinous cuticle form a composite structure for energy storage in jumping by froghopper insects. *BMC biology*, 6(41). Available at: http://www.biomedcentral.com/1741-7007/6/41.

Casari, S.A. & Teixeira, É.P., 2011. Immatures of Syphrea uberabensis guerini Bechyné (Coleoptera, Chrysomelidae, Alticini). *Revista Brasileira de Entomologia*, 55(1), pp.17–26.

Cox, M.L., 1997. The larva of the flea beetle, Mniophila muscorum (KOCH, 1803) (Coleoptera: Chrysomelidae, Alticinae), not a leaf-miner. *Entomologist's Gazette*, 48, pp.275–283.

Crowson, R.A. & Crowson, E.A., 1996. The phylogenetic relations of Galerucinae-Alticinae. In P. H. Jolivet & M. L. Cox, eds. *Chrysomelidae biology. Volume 1: the classification, phylogeny and genetics.* New Yok: SPD Academic Publishing Amsterdam, pp. 97 – 118.

Čížek, P. & Doguet, S., 2008. *Klíč k určování dřepčíků (Coleoptera: Chrysomelidae: Alticinae) Česka a Slovenska*, Nové Město nad Metují: Městské muzeum Nové Město nad Metují.

D'Alessandro, P., Samuelson, A. & Biondi, M., 2016. Taxonomic revision of the genus Arsipoda Erichson , 1842 (Coleoptera , Chrysomelidae) in New Caledonia. *European Journal of Taxonomy*, 230, pp.1–61.

D'Alessandro, P., Urbani, F. & Biondi, M., 2014. Biodiversity and biogeography in Madagascar: revision of the endemic flea beetle genus Neodera Duvivier, 1891 with description of 19 new species (Coleoptera, Chrysomelidae, Galerucinae, Alticini). *Systematic Entomology*, 39(4), pp.710–748. Available at: http://doi.wiley.com/10.1111/syen.12082.

Damaška, A. & Konstantinov, A., 2016. A new species of Cangshanaltica Konstantinov et al., a moss-inhabiting flea beetle from Thailand (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Zootaxa*, 4107(1), pp.93–97.

Deczynski, A.M., 2014. *A preliminary revision of the genus Epitrix Foudras (Coleoptera: Chrysomelidae: Alticinae) in America north of Mexico*. Bachelor's thesis, University of Delaware.

Döberl, M., 2010. Alticinae. In I. Löbl & A. Smetana, eds. *Catalogue of Palaearctic Coleoptera. Vol. 6: Chrysomeloidea*. Stenstrup: Apollo Books, 924 pp., pp. 491–563.

Duckett, C.N., Prathapan, K.D. & Konstantinov, A.S., 2006. Notes on identity, new synonymy and larva of Ivalia Jacoby (Coleoptera: Chrysomelidae) with description of a new species. *Zootaxa*, 68(1363), pp.49–68.

Farrell, B.D., 1998. "Inordinate Fondness" Explained: Why Are There So Many Beetles? *Science*, 281(5376), pp.555–559. Available at: http://www.sciencemag.org/cgi/doi/10.1126/science.281.5376.555.

Ferreira, A. et al., 1984. Cytology and systematical position of Stylopids (= Strepsiptera). *Hereditas*, 100(1), pp.51–52. Available at: http://doi.wiley.com/10.1111/j.1601-5223.1984.tb00103.x.

Flø, D. & Hågvar, S., 2013. Aerial Dispersal of Invertebrates and Mosses Close to a Receding Alpine Glacier in Southern Norway. *Arctic, Antarctic, and Alpine Research*, 45(4), pp.481–490. Available at: http://dx.doi.org/10.1657/1938-4246-45.4.481%5Cnhttp://www.bioone.org/doi/full/10.1657/1938-4246-45.4.481.

Furth, D., 1988. The jumping apparatus of flea beetles (Alticinae) - The metafemoral spring. *Biology of Chrysomelidae*, pp.287–297. Available at: http://link.springer.com/chapter/10.1007/978-94-009-3105-3_17.

Furth, D.D.G., Traub, W. & Harpaz, I., 1983. What makes Blepharida jump? A structural study of the metafemoral spring of a flea beetle. *Journal of Experimental Zoology*, 47, pp.43–47. Available at: http://onlinelibrary.wiley.com/doi/10.1002/jez.1402270107/abstract.

Furth, D.G., 2007. A new genus and species of flea beetle (Coleoptera: Chrysomelidae: Alticinae) from the rainforest canopy in Costa Rica. *Proceedings of the Entomological Society of Washington*, 109(1), pp.90–101. Available at: http://biostor.org/reference/55235%5Cnhttp://entomology.si.edu/StaffPages/FurthD/2007_Laselva_triplehorni.pdf.

Furth, D.G., 1980. Inter-generic differences in the metafemoral apodeme of flea beetles (Chrysomelidae : Alticinae). *Systematic Entomology*, 5, pp.263–271.

Furth, D.G., 1989. Metafemoral Spring Studies of Some Neotropical Genera of Alticinae. *Entomography*, 6, pp.497–510.

Furth, D.G., 1985. Relationships of Palearctic and Nearctic Genera of Alticinae. *Entomography*, 3, pp.375–392.

Furth, D.G., 1979. Zoogeography and host plant ecology of the alticinae of israel, especially Phyllotreta, with description of three new species (Coleoptera: Chrysomelidae). *Israel J. Zool.*, 28(January), pp.1–37.

Furth, D.G. & Savini, V., 1996. Checklist of the Alticinae of Central America , including Mexico (Coleoptera: Chrysomelidae). *Insecta Mundi*, 10(1), pp.45–68.

Furth, D.G. & Suzuki, K., 1998. Studies of Oriental and Australian Alticinae genera based on the comparative morpohology of the metafemoral spring, genitalia and hind wing venation. *Proceedings of the Fourth International Symposium on the Chrysomelidae. Proceedings of XX ICE, Firenze*, 1996, pp.91–124.

Furth, D.G. & Suzuki, K., 1992. The independent evolution of the metafemoral spring in Coleoptera. *Systematic Entomology*, 17(4), pp.341–349. Available at: http://doi.wiley.com/10.1111/j.1365-3113.1992.tb00555.x.

Ge, D. et al., 2011. Anti-predator defence drives parallel morphological evolution in flea beetles. *Proceedings of the Royal Society B*, 278, pp.2133–2141.

Ge, D. et al., 2012. Suprageneric systematics of flea beetles (Chrysomelidae: Alticinae) inferred from multilocus sequence data. *Molecular Phylogenetics and Evolution*, 62(3), pp.793–805. Available at: http://dx.doi.org/10.1016/j.ympev.2011.11.028.

Gómez-Rodríguez, C. et al., 2015. Validating the power of mitochondrial metagenomics for community ecology and phylogenetics of complex assemblages. *Methods in Ecology and Evolution*, 6(8), pp.883–894. Available at: http://dx.doi.org/10.1111/2041-210X.12376.

Gómez-Zurita, J., Hunt, T. & Vogler, A.P., 2008. Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). *Cladistics*, 24(1), pp.34–50.

Haas, F., Gorb, S. & Blickhan, R., 2000. The function of resilin in beetle wings. *Proceedings. Biological sciences / The Royal Society*, 267(1451), pp.1375–81. Available at: http://rspb.royalsocietypublishing.org/content/267/1451/1375.abstract.

Haddad, S. & McKenna, D., 2016. Phylogeny and evolution of the superfamily Chrysomeloidea (Coleoptera: Cucujiformia). *Systematic Entomology*, pp.1–20.

Hamlyn-Harris, R., 1930. Halticinae (Col.) as possible Factors in Natural Control of Mosquitos in Queensland. *Bulletin of Entomological Research*, 21(2), p.159.

Helm, O., 1896. Beiträge zur Kenntniss der Insecten des Bernsteins. *Schriften der Naturforschenden Gesellschaft in Danzig.*, 9(1), pp.220–231.

Horn, G.H., 1889. A Synopsis of the Halticini of Boreal America. *Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Natural Sciences*, 16(3), pp.163–320.

Hua, Y. et al., 2013. The larvae of Altica koreana (Ogloblin) and A. viridicyanea (Baly) (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Zootaxa*, 3694(5), pp.461–470.

Hua, Y. et al., 2015. The larval head structures of Podagricomela shirahatai (Chujo) (Chrysomelidae, Galerucinae, Alticini) and morphological effects of leaf mining. *Journal of Morphology*, 276(4), pp.446–457.

Hua, Y. et al., 2014. The morphology of galerucine and alticine larvae (Coleoptera: Chrysomelidae) and its phylogenetic implications. *Arthropod Systematics and Phylogeny*, 72(2), pp.75–94.

Hunt, T. et al., 2007. A Comprehensive Phylogeny of Beetles Reveals the Evolutionary Origins of a Superradiation Toby. *Science*, 438(2006), pp.1–4.

Chaboo, C.S. et al., 2016. Beetle and plant arrow poisons of the Ju|'hoan and Hai||om San peoples of Namibia (Insecta, Coleoptera, Chrysomelidae; Plantae, Anacardiaceae, Apocynaceae, Burseraceae). *ZooKeys*, 2016(558), pp.9–54.

Chapuis, F., 1875. *Genera des Coléoptères, Vol. 11, Famille des Phytophages* vol. 11. T. Lacordaire, ed., Paris.

de Jong, P. & Nielsen, J., 1999. Polymorphism in a flea beetle for the ability to use an atypical host plant. *Proceedings of the Royal Society B: Biological Sciences*, 266(1414), pp.103–111. Available at: http://apps.webofknowledge.com/full_record.do?product=UA&search_mode=MarkedList&qid=61&SID=T2pGKvAF3UFcnUqx9dT&page=5&doc=44&colName=WOS.

Kemp, T.S., 2005. *The Origin and Evolution of Mammals*, New York: Oxford University Press. Available at: http://onlinelibrary.wiley.com/doi/10.1111/j.1463-6395.2007.00271.x/abstract.

Kim, S.J.I.N. et al., 2003. Comparison between molecular and morphological-based phylogenies of galerucine/alticine leaf beetles (Coleoptera : Chrysomelidae). *Insect Systematics & Evolution*, 34, pp.53–64.

Kimoto, S., 2000. Chrysomelidae (Coleoptera) of Thailand, Cambodia, Laos and Vietnam. VII. Alticinae. *Bull. Inst. Comp. Stud. Intern. Cult. Soc*, 26, pp.103–299.

Kimoto, S., 1965. The Chrysomelidae of Japan and the Ryukyu Islands. VI Subfamily Alticinae I. *Journal of the Faculty of Agriculture*, 13(3).

Kirejtshuk, A.G., Moseyko, A.G. & Ren, D., 2015. Mesozoic Leaf Beetles of the Tribe Mesolpinini trib . nov . (Coleoptera , Chrysomelidae) from the Lower Cretaceous. *Paleontological Journal*, 49(13), pp.1424–1435.

Kirejtshuk, A.G. & Ponomarenko, A.G., 2017. Catalogue of Fossil Coleoptera. *Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*. Available at: https://www.zin.ru/Animalia/Coleoptera/eng/paleosy2.htm.

Kiselev, S. V., 1981. *Pozdnekainozoiskie zhestkokrylye Severo - Vostoka Sibiri.*, Moscow: Paleontologicheskii institut. Nauchnyi sovet po probleme "Puti i zakonomernosti istoricheskogo razvitiia zhivotnykh i rastitel"nykh organizmov.'.

Klebs, R., 1873. Über Bernsteineischlüsse im allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, 51.

Kölsch, G. & Pedersen, B.V., 2008. Molecular phylogeny of reed beetles (Col., Chrysomelidae, Donaciinae): The signature of ecological specialization and geographical isolation. *Molecular Phylogenetics and Evolution*, 48(3), pp.936–952.

Konstantinov, Alexander S.; Baselga, Andrés; Grebennikov, Vasily V.; Prena, Jens; Lingfalter, S.W., 2011. *Revision of the Palearctic Chaetocnema species (Coleoptera: Chrysomelidae: Galerucinae: Alticini)*,

Konstantinov, A. et al., 2013. Moss-inhabiting flea beetles (Coleoptera: Chrysomelidae: Galerucinae: Alticini) with description of a new genus from Cangshan, China. *Journal of Natural History*, pp.37–41.

Konstantinov, A.S., 2016. Possible living fossil in Bolivia: A new genus of flea beetles with modified hind legs (Coleoptera, Chrysomelidae, Galerucinae, Alticini). *ZooKeys*, 592, pp.103–120. Available at: http://zookeys.pensoft.net/articles.php?id=8180.

Konstantinov, A.S. & Duckett, C.N., 2005. New species of Clavicornaltica Scherer (Coleoptera: Chrysomelidae) from continental Asia. *Zootaxa*, 1037, pp.49–64.

Konstantinov, A.S. & Konstantinova, A.A., 2011. New genus and species of flea beetles (Coleoptera, Chrysomelidae, Galerucinae, Alticini) from Puerto Rico, with comments on flea beetle diversity in the West Indies and a key to the West Indian Monoplatini genera. *ZooKeys*, 155, pp.61–87.

Konstantinov, A.S. & Lourdes Chamorro-Lacayo, M., 2006. A New Genus of Moss-inhabiting Flea Beetles (Coleoptera: Chrysomelidae) from the Dominican Republic. *Coleopterists Bulletin*, 60(4), pp.275–290.

Konstantinov, A.S. & Vandenberg, N.J., 1996. Handbook of Palearctic Flea Beetles (Coleoptera: Chrysomelidae: Alticinae). *Contributions on Entomology, International,*, 1(3), pp.233–439. Available at: https://books.google.cz/books?id=aobDYgEACAAJ.

Kreft, H. & Jetz, W., 2010. A framework for delineating biogeographic regions based on species distributions. *Journal of Biogeography*, 37, pp.2029–2053.

Kuzmina, S.A., 2015. Quaternary insects and environment of northeastern Asia. *Paleontological Journal*, 49(7), pp.679–867. Available at: http://link.springer.com/10.1134/S0031030115070011.

Lee, C. et al., 2011. A Review of Phyllotreta Chevrolat in Taiwan (Coleoptera : Chrysomelidae : Galerucinae : Alticini). , 50(4), pp.525–533.

Legalov, A.A., 2013. Review of the family Anthribidae (Coleoptera) from the Jurassic of Karatau: subfamily Protoscelinae. Genus Protoscelis Medvedev. *Paleontological Journal*, 47(3), pp.292–302.

Lever, R., 1930. A new endoskeletal organ in the hind leg of the Halticinae. *Zoologischer Anzeiger*, 92, pp.287–288.

Lingafelter, S.W. & Konstantinov, A.S., 1999. The monophyly and relative rank of alticine and galerucine leaf beetles: a cladistic analysis using adult morphological characters (Coleoptera: Chrysomelidae). *Insect Systematics & Evolution*, 30(4), pp.397–416.

Linzmeier, A.M. & Konstantinov, A.S., 2012. A new genus of leaf litter inhabiting Neotropical Monoplatina (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Zootaxa*, (3260), pp.19–32.

Lyons, R.E. et al., 2011. Molecular and functional characterisation of resilin across three insect orders. *Insect Biochemistry and Molecular Biology*, 41, pp.881–890.

Maddison, W.P. & Maddison, D.R., 2017. Mesquite: a modular system for evolutionary analysis. Available at: http://mesquiteproject.org.

Maulik, F.Z.S., 1929. On the Structure of the Hind Femur in Halticine Beetles. *Proceedings of the Zoological Society of London*, 99, pp.305–308.

McKenna, D. et al., 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, 40, pp.835–880.

Mebs, D., Brünnig, F. & Pfaff, N., 1982. Preliminary studies of the chemical properties of the toxic principle from Diamphidia nigroornata larvae, a source of Bushman arrow poison. *Journal of Ethnopharmacology*, 6, pp.1–11.

Medvedev, L.N., 2010. New and poorly known Alticinae (Coleoptera: Chrysomelidae) from New Guinea and islands of Southeast Asia. *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, 3, pp.291–304. Available at: http://www.naturkundemuseum-bw.de/sites/default/files/publikationen/serie-a/ans03-14medvedev.pdf.

Medvedev, L.N., 1997. New records and new species of Chrysomelidae from Arabia. *Fauna of Saudi Arabia*, 16, pp.319–326.

Medvedev, L.N., 1996. Review of the flea-beetle genus Clavicornaltica SCHERER , 1974 (Coleoptera: Chrysomelidae, Alticinae). *Zeitschrift für Entomologie*, 17(8), pp.137–148.

Michels, J., Appel, E. & Gorb, S.N., 2016. Functional diversity of resilin in Arthropoda. *Beilstein Journal of Nanotechnology*, 7, pp.1241–1259. Available at: http://www.beilstein-journals.org/bjnano/content/7/1/115.

Mohamedsaid, M.S., 2016. *Catalogue of the Malaysian Chrysomelidae (Insecta: Coleoptera)* Series Fau., Sofia-Moscow: Pensoft.

Mohamedsaid, M.S., 2009. Chrysomelidae of the Lesser Sunda Islands : Wallace ' s Line and the crossing of worlds. *Research on Chrysomelidae*, 2, pp.57–104.

Morais, A.N.A.C.C., Ribeiro-costa, C.S. & Linzmeier, A.M., 2016. On the taxonomy of the Brazilian flea beetle genus Miritius Bechyné & Bechyné (Coleoptera: Chrysomelidae: Galerucinae: Alticini: Monoplatina) with description of two new species. , 4067(3), pp.334–344.

Moseyko, A.G., Kirejtshuk, A.G. & Nel, A., 2010. New genera and new species of leaf beetles (Coleoptera: Polyphaga: Chrysomelidae) from Lowermost Eocene French amber. *Annales de la Société entomologique de France*, 46((1-2)), pp.116–123.

Nadein, K. & Betz, O., 2016. Jumping mechanisms and performance in beetles. I. Flea beetles (Coleoptera: Chrysomelidae: Alticini). *The Journal of Experimental Biology*, 219(13), pp.2015–2027. Available at: http://jeb.biologists.org/lookup/doi/10.1242/jeb.140533.

Nadein, K.S., 2013. Catalogue of Alticini genera of the World (Coleoptera: Chrysomelidae). *Beetles and Coleopterists website, Zoological Institute, Saint-Petersburg*. Available at: https://www.zin.ru/animalia/coleoptera/eng/alticini.htm.

Nadein, K.S., 2010. New Taxa of Chrysomelidae (Insecta: Coleoptera) from Rovno Amber, Late Eocene. *Acta Geologica Sinica*, 84(4), pp.772–782. Available at: http://www.ncbi.nlm.nih.gov/pubmed/15003161.

Nadein, K.S., 2009. Revision of the genus Mniophila Stephens, 1831. *BBeiträge zur Entomologie*, 59, pp.103–131.

Nadein, K.S., Perkovsky, E.E. & Moseyko, A.G., 2016. New Late Eocene Chrysomelidae (Insecta: Coleoptera) from Baltic, Rovno and Danish ambers. *Papers in Palaeontology*, 2(1), pp.117–137.

Orlova-Bienkowskaja, M.J., 2015. Epitrix papa sp. n. (Coleoptera: Chrysomelidae: Galerucinae: Alticini), previously misidentified as Epitrix similaris, is a threat to potato production in Europe. *European Journal of Entomology*, 112(4), pp.824–830.

Papadopoulou, A., Cardoso, A. & Gómez-Zurita, J., 2013. Diversity and diversification of Eumolpinae (Coleoptera: Chrysomelidae) in New Caledonia. *Zoological Journal of the Linnean Society*, 168(3), pp.473–495.

Perger, R., 2013. Did the genus Parandrocephalus Heller, 1916 (Coleoptera, Cerambycidae, Callichromatini) cross the Wallace line? The taxonomic status of Parandrocephalus blairi Bentanachs & Vives 2009 and a new subgenus of Hexamitodera Heller, 1896, with notes on converge. *ZooKeys*, 293, pp.77–89.

Petitpierre, E., 2006. A new contribution to the cytogenetic knowledge of Alticinae (Coleoptera, Chrysomelidae). *Hereditas*, 143(2006), pp.58–61.

Petitpierre, E., 1997. The value of cytogenetics for the taxonomy and evolution of Leaf Beetles (Coleoptera, Chrysomelidae). *Miscellania Zoologica*, 20(1), pp.9–18.

Petitpierre, E., Segarra, C. & Juan, C., 1993. Genome size and chromosomal evolution in leaf beetles (Coleoptera, Chrysomelidae). *Hereditas*, 119(1), pp.1–6.

Poinar, G., 2005. A Cretaceous palm bruchid, Mesopachymerus antiqua, n. gen., n. sp. (Coleoptera: Bruchidae: Pachymerini) and biogeographical implications. *Proceedings of the Entomological Society of Washington*, 107(2), pp.392–397.

Prathapan, K.D. & Chaboo, C.S., 2011. Biology of Blepharida-group flea beetles with first notes on natural history of Podontia congregata Baly, 1865 an endemic flea beetle from southern India (Coleoptera, Chrysomelidae, Galerucinae, Alticini). *ZooKeys*, 157, pp.95–130.

Rasnitsyn, A.P. & Ross, A.J., 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. *Bulletin of the Natural History Museum, London (Series Geology)*, 56(1), pp.21–24.

Reid, C.A.M., 1995. A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). *Biology, Phylogeny and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson*, 2, pp.559–631.

Reid, C.A.M., 1988. Bellaltica Reid, a New Genus of Alticinae (Coleoptera: Chrysomelidae) from South-West Western Australia. *Coleopterists Bulletin*, 42(3), pp.219–231.

Reid, C. a. M. & Beatson, M., 2015. Disentangling a taxonomic nightmare: a revision of the Australian, Indomalayan and Pacific species of Altica Geoffroy, 1762 (Coleoptera: Chrysomelidae: Galerucinae). *Zootaxa*, 3918(4), pp.503–551.

Riley, E.G., Clark, S.M. & Seeno, T.N., 2003. *Catalog of the leaf beetles of America North of Mexico (Coleoptera: Megalopididae, Orsodacnidae and Chrysomelidae, excluding Bruchinae).*, Coleopterists Society.

Ruan, Y.-Y. et al., 2015. Penghou, a new genus of flea beetles from China (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Zootaxa*, 3973(2), p.300. Available at: http://biotaxa.org/Zootaxa/article/view/zootaxa.3973.2.5.

Samuelson, B.G.A., 1969. Alticinae of New Guinea, III. Schenklingia and allies (Coleoptera: Chrysomelidae). *Pacific Insects*, 11(1), pp.33–47.

Samuelson, G.A., 1965. Alticinae of New Guinea I. Micrepitrix. *Pacific Insects*, 7(2), pp.219–224.

Samuelson, G.A., 1971. Alticinae of New Guinea IV. *Pacific Insects*, 13(3–4), pp.513–518.

Samuelson, G.A., 1989. Pollen feeding in Alticinae (Chrysomelidae). *Entomography*, 6, pp.407–411.

Santiago-Blay, J., 1994. Paleontology of leaf beetles. In P. H. Jolivet, M. L. Cox, & E. Petitpierre, eds.

Novel aspects of the biology of Chrysomelidae SE - 1. Series Entomologica. Springer Netherlands, pp. 1–68. Available at: http://dx.doi.org/10.1007/978-94-011-1781-4_1.

Santiago-Blay, J.A., 2004. Leaf-mining chrysomelids. In P. H. Jolivet, J. A. Santiago-Blay, & M. Schmitt, eds. *New developments in the biology of Chrysomelidae*. Hague: Academic Publishing bv, The Netherlands, pp. 305–306.

Santiago-Blay, J.A. & Craig, P.R., 1999. Preliminary Analysis of Chrysomelid palaeodiversity, with new record and new species from Dominican amber (early to middle Miocene). In M. L. Cox, ed. *Advances in Chrysomelidae Biology.* Amsterdam: SPB Academic Publishing, pp. 17–24.

Savini, V. & Escalona, H.E., 2005. A new species of Longitarsus Latreille, 1825 from Mexico (Coleoptera, Chrysomelidae, Alticinae, Longitarsini). *Zootaxa*, 7(956), pp.1–7.

Scudder, S.H., 1876. Fossil Coleoptera from the Rocky Mountain Tertiaries. *Bulletin of the United States Geological and Geographical Survey of the Territories*, 2(May).

Seeno, T.N. & Wilcox, J.A., 1982. *Leaf beetle genera (Coleoptera, Chrysomelidae)*, Entomography Publications.

Segarra, C. & Petitpierre, E., 1989. Cytogenetic diversity of the European Psylliodes flea-beetles (Coleoptera, Chrysomelidae). *Hereditas*, 110(December), pp.169–174.

Segarra, C. & Petitpierre, E., 1988. Chromosomes of sixteen European species of Longitarsus flea-beetles (Coleoptera, Chrysomelidae). *Genetica*, 76(3), pp.203–208.

Segarra, C. & Petitpierre, E., 1982. Preliminary data on the chromosomes of European Alticinae. *Spixiana*, 7, pp.29–37.

Scherer, G., 1973. Alticinae of Oceania. *Pacific Insects Monographs*, 30, pp.1–165.

Scherer, G., 1974. Clavicornaltica, a new genus from Ceylon (Coleoptera: Chrysomelidae: Alticinae). *Revue Suisse de Zoologie.*, 81(1), pp.57–68. Available at: http://www.biodiversitylibrary.org/part/75989 [Accessed November 19, 2015].

Scherer, G., 1983. Diagnostic key for the Neotropical alticine genera (Coleoptera: Chrysomelidae: Alticinae). *Entomologische Arbeiten - Museum G. Frey*, v. 31/32.

Scherer, G., 1988. The Origins of the Alticinae. In P. H. Jolivet, E. Petitpierre, & T. H. Hsiao, eds. *Biology of Chrysomelidae*. Dordrecht: Kluwer Academic Publishers, pp. 115–130.

Schmitt, M., 2004. Jumping flea beetles: structure and performance (Insecta, Chrysomelidae, Alticinae). *New Developments in the Biology of Chrysomelidae*, pp.161–169.

Smith, E.H., 1985. *Revision od the Genus Phyllotreta Chevrolat of America North of Mexico, Part I. The Maculate Species (Coleoptera: Chrysomelidae: Alticinae)*, Chicago: Field Museum of Natural History.

Sprecher-Uebersax, E. et al., 2008. Revision of the genus Benedictus Scherer (Insecta : Coleoptera : Chrysomelidae: Galerucinae). In *Biodiversität und Naturausstattung im Himalaya, Bd. III*. pp. 475–514.

Takizawa, H., 2005. Supra-generic subdivisions of the subfamily Alticinae based on larval characters, with descriptions of larvae of Hispaniolan species (Coleoptera: Chrysomelidae). *Insecta Matsumurana*, 62, pp.187–206.

Toussaint, E.F.A. et al., 2016. The peril of dating beetles. *Systematic Entomology*, 42(1), pp.1–10. Available at: http://doi.wiley.com/10.1111/syen.12198.

Vencl, F. V & Morton, T.C., 1998. The shield defense of sumac flea beetle, Blepharida rhois (Chrysomelidae: Alticinae). *Chemoecology*, 8, pp.25–32.

Virkki, N. & Santiago-Blay, J.A., 1996. Chromosomes of some Puerto Rican flea beetles (Coleoptera: Chrysomelidae: Alticinae): multiple cytogenetic evolutionary tendencies in the Neotropics. *Journal of Zoological Systematics and Evolutionary Research*, 34, pp.113–119.

Virkki, N. & Santiago-Blay, J.A., 1993. Trends of karyotype evolution in neotropical Oedionychina (Coleoptera: Chrysomelidae: Alticinae). *Hereditas*, 119(3), pp.263–283.

Westwood, J.O., 1854. Contributions to fossil entomology. *The Quarterly journal of the Geological Society of London.*, 10, pp.378–396.

Woollard, J.M.R., Fuhrman, F.A. & Mosher, H.S., 1984. The Bushman arrow toxin, diamphidia toxin: Isolation from pupae of Diamphidia nigro-ornata. *Toxicon*, 22(6), pp.937–946.