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Evolution of histeroid beetles (Coleoptera: Histeroidea): phylogenetics,
fossil record and life histories

Evoluce mršníkovitých brouků (Coleoptera: Histeroidea): fylogeneze,
fosilní záznam a životní strategie

Bachelor´s thesis

Supervisor: Mgr. Martin Fikáček, Ph. D.

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl 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. 2021

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Abstrakt

Mršníkovití brouci (Coleoptera: Staphyliniformia: Histeroidea) představují důležitou linii brouků, která je známá pro svou morfologickou rozmanitost a široké spektrum obývaných stanovišť. V této práci shrnuji dostupné informace ohledně fylogenetické pozice této skupiny brouků a o jejich biologii a ekologii. Zvláště se zabývám současnými představami o evoluční historii všech čtyř čeledí spadajících do Histeroidea (Histeridae, Cretohisteridae, Synteliidae a Sphaeritidae) a o fylogenetických vztazích uvnitř čeledi Histeridae. Shrnuji také dostupné poznatky o diverzitě těchto brouků ve fosilním záznamu a uvádím seznam všech doposud popsaných fosilních druhů. Mršníkovití brouci prošli četnými změnami stanovištních specializací, což často způsobilo zjevné změny v jejich morfologii a chování. V některých případech změna habitatu zřejmě vedla ke zvýšení rychlosti diverzifikace dané linie. V této práci se snažím propojit dostupná fylogenetická, paleontologická a ekologická data s cílem poskytnout shrnutí evoluční historie skupiny Histeroidea.

Klíčová slova: Histeroidea, Histeridae, Synteliidae, Sphaeritidae, Cretohisteridae, evoluce, fylogeneze, fosilie, životní strategie, habitatové změny

Abstract

Histeroid beetles (Coleoptera: Staphyliformia: Histeroidea) represent an important lineage of beetles, known for a rich diversity of body forms and inhabited environments. In this thesis, I summarize available information about their position in the beetle tree of life and the available information about their ecology and biology. I specifically address current ideas about the evolution of the four histeroid families (Histeridae, Cretohisteridae, Synteliidae and Sphaeritidae) and the internal phylogeny of the Histeridae. To understand the available data about the past diversity of the group, I provide a summary of all described fossil species. The group has undergone numerous habitat shifts, often connected with apparent morphological and behavioural adaptations, some of which likely increased the diversification rate of respective lineages. This thesis aims to connect the available phylogenetic, fossil and ecological data to provide a summary of the evolutionary history of the lineage.

Key words: Histeroidea, Histeridae, Synteliidae, Sphaeritidae, Cretohisteridae, evolution, phylogeny, fossils, life history strategies, habitat shifts

Contents

1 Introduction

In his famous book *The Naturalist on the River Amazon*, Henry Walter Bates (1863) reflected on his 11 year long expedition to the Amazon basin and he stated the following:

> "*It is curious to observe how some small groups of insects exhibit the most diversified forms and habits – one set of species being adapted by their structure for one set of functions in nature, and another set, very closely allied, for an opposite sphere of action. Thus the Histeridae (…) are most diversified in structure and habits in the Amazons region nevertheless, all the forms preserve in a remarkable degree the essential characters of the family. Several families of insects show similar diversities of adaptation amongst their species, but none, I think, to the same extent as the Histeridae (…). The facts presented by such groups in the animal kingdom must be taken into account in any explanation of the way the almost infinite diversity of the forms of life has been brought about on this wonderful earth.*"

Histeridae, or clown beetles (named after their flattened tibia resembling wide clown's trousers), represent a group of beetles (Coleoptera), belonging to the polyphagan superfamily Histeroidea. Histeroidea contains four families – extinct Cretohisteridae, species-poor Synteliidae and Sphaeritidae and the very diverse Histeridae. They are all small to medium sized beetles with a compact body, mostly sharing predaceous lifestyle.

Their more than 4500 species can be found in surprisingly diverse environments – animal faeces and carcasses, forest litter, subcortical space, tunnels of wood-boring beetles, rotting cacti and other succulents, decomposing plant or fungi material, mammal burrows and bird nests, colonies of ants and termites, subterranean cavities and caves, sand dunes etc. Many species, or even larger evolutionary lineages, live only in a single type of habitat. As Bates explained, they have evolved unique morphological adaptations, or even changed their entire body shape, based on the environment they live in. This has made the group an ideal model for studying evolutionary processes connected with habitat specializations.

Some of the first beetles I ever collected were a few specimens of *Margarinotus purpurascens* – in cow dung during a school expedition to Switzerland in 2013. I have since collected many other species of Histeridae and I quickly found the group fascinating. In fact, it has led me to appreciate the beautiful diversity of life's forms. In this thesis, I try to follow the instruction of H. W. Bates by studying histeroid beetles with the intent to explain a little bit about *"the way the almost infinite diversity of the forms of life has been brought about on this wonderful earth."*

2 Taxonomy and phylogeny

The beetle superfamily Histeroidea, as we now understand it, comprises of four families – Sphaeritidae, Synteliidae, Cretohisteridae and Histeridae (Zhou et al. 2018) (Figure 1).

Sphaeritidae and Synteliidae are relatively small groups (both containing only one genus with six and seven described extant species, respectively). Cretohisteridae is an extinct lineage known from a single Early Cretaceous fossil (age is estimated at 125 mya). Histeridae is a diverse family containing ten currently recognised subfamilies (Figure 2) with more than 4500 species (Beutel et al. 2016; Mazur 2011; Zhou et al. 2018, 2020). The currently recognised taxa of Histeroidea are summarized in Table 1. Nomenclature in this thesis follows Mazur (2011). The authorship of taxa mentioned in this thesis but not covered by Mazur's catalogue (extinct, described later or belonging to Synteliidae and Sphaeritidae) is summarized in chapter 7 (Attachments).

Table 1. Summary of the species diversity of families and subfamilies of Histeroidea (according to Beutel et al. (2016), Zhou et al. (2018, 2020)). † – extinct taxon

Family	Subfamily	Genera	Species
Sphaeritidae		1	6
Synteliidae		1	7
Cretohisteridae†		1†	1†
Histeridae	Abraeinae (incl. Trypanaeini and Trypeticini)	30	>650
	Antigracilinae†	1†	1†
	Chlamydopsinae	13	>175
	Dendrophilinae	33	>460
	Haeteriinae	111	>330
	Histerinae	143	>1930
	Niponiinae	1	>20
	Onthophilinae	7	>80
	Saprininae	51	>700
	Tribalinae	11	>210
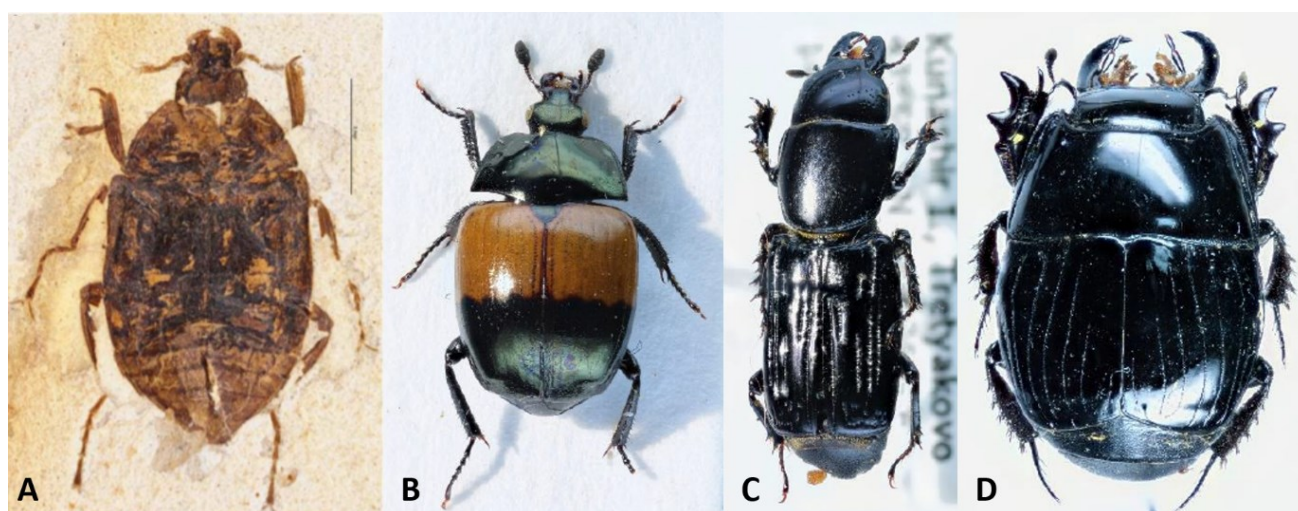
Figure 1. General habitus of adults of Histeroidea families. A – Cretohisteridae (adopted from Zhou et al. (2018)), B – Sphaeritidae, C – Synteliidae, D – Histeridae
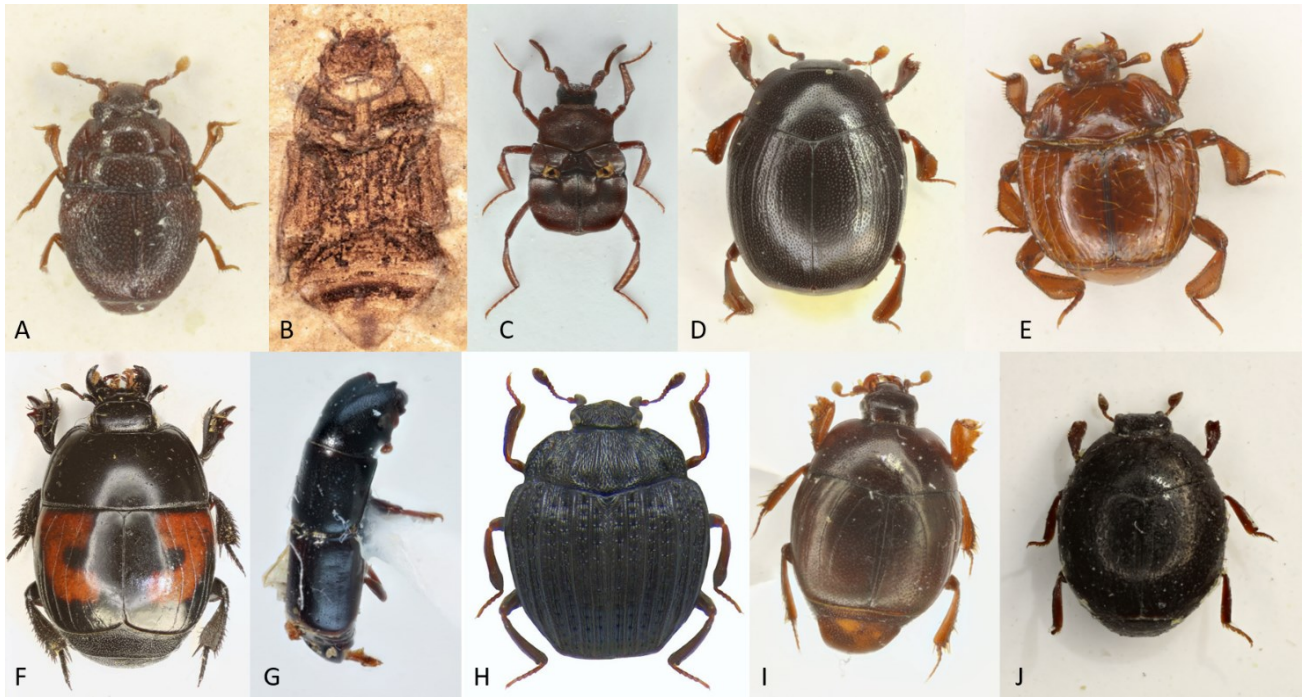
Figure 2. General habitus of Histeridae subfamilies. A – Abraeinae, B – Antigracilinae (adopted from Zhou et al. (2020)), C – Chlamydopsinae, D – Dendrophilinae, E – Haeteriinae, F – Histerinae, G – Niponiinae, H – Onthophilinae, I – Saprininae, J – Tribalinae

According to Beutel & Leschen (2005), Beutel et al. (2016) and Ohara (1994) the main synapomorphies of the Histeroidea superfamily include:

- Adult characters:
    - 3-segmented compact antennal club
    - prominent acute mandibles
    - truncate elytra (covering 6 abdominal segments at most)
    - enlarged clypeus
    - ovipositors with scoop-like gonoxites bearing mesal styli
    - carnivorous feeding habit
- Larvae characters:
    - posteriorly shifted posterior tentorial pits (Beutel et al. (2016) erroneusly states they are also widely separated, however they are fused or only narrowly separated (Beutel 1999); Figure 3A)
    - absence of maxillary fossa
    - two or three inner appendages (sensoria) of antenna (Figure 3 – sap)
    - cardo not recognisable and separate sclerite (fused with stipes or reduced)
    - membranous mentum
    - dense preoral filter apparatus formed by long hairs on hypopharynx and maxillary bases (Kovarik & Passoa 1993) (Figure 3 – pof)
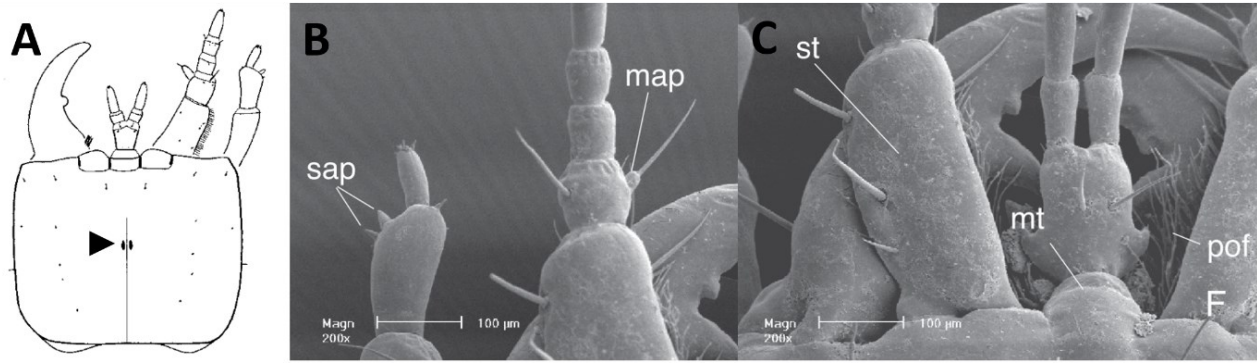
Figure 3. Histeroidea head morphology of larvae. A – *Syntelia histeroides*; black arrow – posterior tentorial pits; B-C – *Onthophilus* sp.; sap – sensorial appendages, pof – preoral filter apparatus. Adopted from Beutel & Leschen (2005) and Newton (1991)

The histeroid families are sometimes included in Hydrophiloidea *sensu lato*, within which they form a monophyletic clade sister to the aquatic hydrophiloid families (Lawrence & Newton 1982; McKenna et al. 2019; Zhang et al. 2018). In this thesis I follow the use of the concept of two separate superfamilies – Hydrophiloidea *sensu stricto* and Histeroidea. They are currently placed within the infraorder Staphyliniformia, together with Staphylinoidea (Beutel, 2016). The review of phylogenetic studies on the group follows hereafter.

2.1   Histeroidea on the beetle tree of life

Beetles (Coleoptera) represent the most species-rich animal order, containing over 25 % of all described animal species (Slipinski et al. 2011). The first definitive beetle fossils come from the Early Permian time period. The stem age of beetles is estimated to date back to the Late-Carboniferous to Early Permian (Hunt et al. 2007; McKenna et al. 2015b, 2019; Misof et al. 2014; Zhang et al. 2018), although Toussaint et al. (2017) suggested it to be as old as Mid-Carboniferous. According to the latest study, the order is divided into two main clades – one containing the suborders Archostemata, Myxophaga and Adephaga, the other grouping all lineages of the suborder Polyphaga (McKenna et al. 2019).

Histeroids are undoubtebly representatives of the polyphagan clade (McKenna et al. 2015b, 2019; Zhang et al. 2018). According to the vast majority of studies they are sister group to the superfamily Hydrophiloidea *s.s.* (McKenna et al. 2015b,a, 2019; Zhang et al. 2018). Some analyses placed the group as sister to various clades of Staphylinoidea (Bocak et al. 2013; Korte et al. 2004), but these hypotheses were not confirmed by the latest analyses based on large sets of nuclear protein-coding genes which show the sister relationship between Histeroidea and Hydrophiloidea with strong support (Zhang et al. 2018, McKenna et al. 2019). The two superfamilies also share some important synapomorphies, such as a symetrical antennal club, elongate shape of the scapus and pedicellus, larval labrum fused to clypeus etc. (Beutel & Leschen 2005). The precise phylogenetic position of Histeroidea+Hydrophiloidea is still not fully understood, with even the most recent studies showing incongruent results (see Table 2).

McKenna et al. (2015a) placed the clade as sister to Staphylinoidea (therefore supporting the monophyletic state of the Staphyliniformia infraorder). The analysis by McKenna et al. (2015b) resulted in conflicting topologies. Bayesian analyses recovered Histeroidea+Hydrophiloidea as sister to Scarabaeoidea and found Staphylinoidea as a sister group to the above three lineages. In contrast, a maximum likelihood analyses recovered monophyletic Staphyliniformia as sister to the Scarabaeoidea. Results of Zhang et al. (2018) show that the Staphilinoidea+Scarabaeoidea form a monophyletic clade, which is sister to Histeroidea+Hydrophiloidea. Robust genomic analysis by McKenna et al. (2019) revealed the same topology.

Table 2. Studies dealing with phylogenetic position of Histeroidea. Hist – Histeroidea, Hydr – Hydrophiloidea, Sta – Staphylinoidea, Sca – Scarabaeoidea

Study	Analysed group	Genes	Nr of species	Topology	Histeroidea age (mya)	
					stem	crown
McKenna et al. (2015a)	Staphyliniformia + Scarabaeiformia	2 (CAD, 28s)	279	((Hist+Hydr)+Sta)+Sca	-	-
McKenna et al. (2015b)	Coleoptera	8 (nuclear)	367	Bayesian: ((Hist+Hyd)+Sca)+Sta Maximum likelihood: ((Hist+Hyd)+ Sta)+ Sca	168.31 (187.52 to 151.09)	131.60 (156.60 to 106.09)
Zhang et al. (2018)	Coleoptera	95 (nuclear)	374	(Hist+Hyd)+(Sta+Sca)	Ca. 203 to 179	-
McKenna et al. (2019)	Coleoptera	4818 (nuclear)	146	(Hist+Hyd)+(Sta+Sca)	Late Triassic to Early Jurassic	-

The aforementioned studies date the origin of the Histeroidea within the late Triassic to the Jurassic period. Toussaint et al. (2017) estimates an even earlier origin, in the Early Triassic or even Late Permian period. The first definitive Histeroidea fossils date back to 125 mya and represent the families Cretohisteridae and Histeridae (Zhou et al. 2018, 2020). By that time, all four families must have been present, as Sphaeritidae and Synteliidae radiated before the split of Histeridae and Cretohisteridae (which are sister groups; see the following chapter).

2.2 Histeroidea inner phylogenetic relationships

As mentioned before, the Histeroidea are formed by four families – Sphaeritidae, Synteliidae, extinct Cretohisteridae, and Histeridae, the largest family. Sharp & Muir (1912) first proposed the connection between the three extant families based on similarities in aedeagus morphology.

Since then, there have been several studies focused on the phylogeny of Histeroidea or Histeridae only (Caterino & Vogler 2002; Ohara 1994; Ślipiński & Mazur 1999; Zhou et al. 2018, 2020). Other works have analysed the phylogeny of higher groups, but included a significant number of histeroid taxa as well (Caterino et al. 2005; Hansen 1997; McKenna et al. 2015a).

According to Zhou et al. (2018), Cretohisteridae are the sister group to Histeridae based on the analysis of a morphological dataset. This was later confirmed by Zhou et al. (2020).

The phylogenetic position of the other two families (Sphaeritidae and Synteliidae) is not entirely clear (Figure 4). Some works – mostly those based, at least partially, on morphological characters – place Sphaeritidae as sister to Synteliidae+Histeridae (Caterino & Vogler 2002; Hansen 1997; Zhou et al. 2018). Others, mostly those using DNA data only, place Synteliidae as sister to Sphaeritidae+Histeridae (Bocak et al. 2013; Hunt et al. 2007; McKenna et al. 2015a,b; Zhou et al. 2020). Caterino et al. (2005) recovered both topologies in various analyses of the same DNA and morphology dataset.
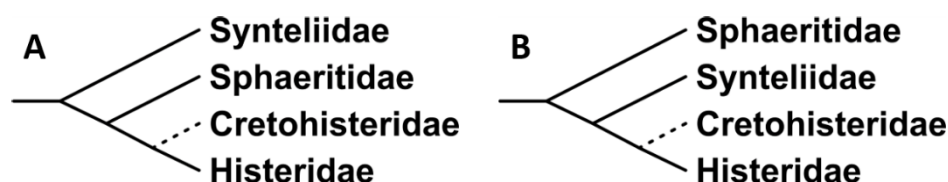

Figure 4. Alternative hypotheses about the phylogenetic relationships of histeroid families. A – proposed by Bocak et al. (2013), Caterino et al. (2005), Hunt et al. (2007) Mckenna et al. (2015a,b), Zhou et al. (2020); B – proposed by Caterino & Vogler (2002), Caterino et al. (2005), Hansen (1997), Zhou et al. (2018)

Most recent and robust studies have agreed on placing Sphaeritidae as the sister group to Histeridae+Cretohisteridae. It is worth noting, that the sampling of Sphaeritidae and Synteliidae was very limited in all of the mentioned studies – only one species of each family was included (except of Zhou et al. (2018) who used two species of Sphaeritidae). Using additional *Sphaerites* and *Syntelia* species might help to improve the robustness of the histeroid tree of life.

2.3 Histeridae phylogeny

Zhou et al. (2020) published the most recent and comprehensive study focused on the internal Histeridae phylogeny. The authors used a dataset of four genes and 50 taxa representing 10 of the 11 then recognised subfamilies with sequences provided by previous studies. The second dataset contained 69 morphological adult characters of 40 extant and 6 extinct taxa of all then recognised subfamilies. A combined DNA and morphology analysis was also performed. The analyses by Zhou et al. (2020) and others revealed several congruently supported monophyletic clades within Histeridae. Topology recovered by Zhou et al. (2020) is illustrated in Figure 5. This subchapter presents the results of Zhou et al. (2020) unless stated otherwise.

Saprininae have been repeatedly recovered as monophyletic by Zhou et al. (2020) as well as by other studies (Caterino & Vogler 2002; Lackner 2014a; Lackner et al. 2019; McKenna et al. 2015a).

Both Zhou et al. (2020) and McKenna et al. (2015a) confirm the existence of a sister clade to Saprininae referred to as "Histeromorphae". The clade contains the subfamilies Histerinae, Tribalinae, Haeteriinae and Chlamydopsinae and represents the crown group of Histeridae. Histerinae is a paraphyletic group, as they also include the monophyletic inquilinous Haeteriinae (also confirmed by Caterino & Tishechkin (2015)), part of polyphyletic Tribalinae (which are distributed within "Histeromorphae") and possibly also the monophyletic group of Austro-Pacific myrmecophilous Chlamydopsinae. The authors did not make any taxonomic adjustments within the "Histeromorphae" clade as several key taxa were not included in the analysis.

The subfamily Abraeinae was strongly supported as monophyletic when the lineages with cylindrical body, earlier classified as Trypanaeinae and Trypeticinae were included. That supported the findings of Caterino & Vogler (2002) and McKenna et al. (2015a). Based on this result, Zhou et al. (2020) downgraded Trypanaeinae and Trypeticinae to tribe level and included them within Abraeinae subfamily.

The position of the cylindrical-bodied and monophyletic subfamily Niponiinae could not be resolved and particular analyses placed it either within Teretriini (Abraeinae) or Paromalini (Dendrophilinae). Unfortunatelly molecular data are not yet available for the subfamily.

The Onthophilinae were found polyphyletic, forming two separate clades: Onth I – Onthophilus+Epiechinus (two most diverse Onthophilinae genera) as inner group of part of Dendrophilinae (Dend II) and Onth II – *Peploglyptus* as sister to the tribaline genus *Stictostix*. Caterino (2004) states that the position of *Peploglyptus* is unclear and proposes its connection to *Stictostix,* stating they both could be well assigned to either Onthophilinae or Tribalinae under their vague definitions. Kovarik (1994) also confirms the sister relationship of *Peploglyptus* and *Stictostix* based on adult morphology.

Dendrophilinae appeared to be paraphyletic and formed two lineages (Dend I and Dend II). Dend I contains the tribes Anapleini and Dendrophilini and is sister to Saprininae+"Histeromorphae". Dend II includes Paromalini and Bacaniini and also the Onthophilinae genera *Onthophilus* and *Epiechinus* and were placed as sister to Dend I+Saprininae+"Histeromorphae".

The extinct subfamily Antigracilinae was recovered as sister to all other histerids.

It is obvious that the systematics and higher classification of the Histeridae will need major revisions, mainly regarding the subfamilies Onthophilinae, Dendrophilinae, Tribalinae and Histerinae. The rank and phylogenetic position of Haeteriinae, Chlamydopsinae and Niponiinae might as well need changes. In order to clarify the needed adjustments, it is necessary to extend the molecular dataset by sequencing additional genes and including important taxa (for example *Niponius*, *Baconia*, *Platylomalus* etc.).
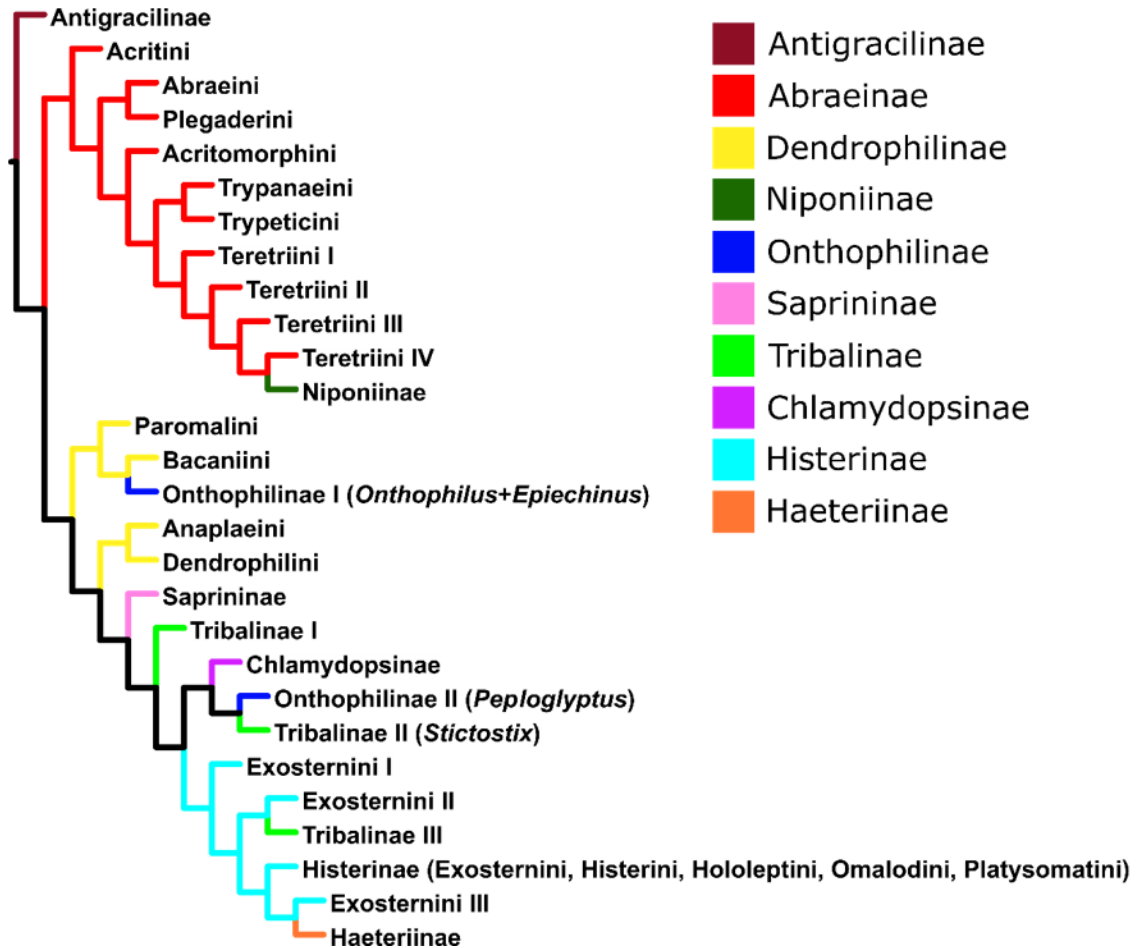
Figure 5. Histeridae phylogeny according to Zhou et al. (2020)

3   Fossil record of the Histeroidea

Fossils represent an important tool for evolutionary studies. When correctly dated and correctly placed into a phylogeny, they provide important information about the minimum age of a certain lineage, its morphological characters or ecological adaptations. This information can be used for dating phylogenetic trees and reconstructing the evolution of life-history strategies (Forest 2009).

Only a limited number of relatively young (Cenozoic) fossil species of Histeroidea was described in the 19th and 20th centuries. These were described in three studies: Heer (1862), Piton & Théobald (1935) and Handschin (1944). In recent years, numerous articles describing new fossil species have been published. New species are being regularly discovered, especially in the Burmese amber, which is significant by its age (ca. 99 million years old) and inclusion density. Histeroid species are relatively scarce in Burmese amber but can be accumulated when a large number of inclusions is inspected (Zhung Tian, pers. comm.). Table 3 summarizes all Histeroidea fossil species described to date. Examples of fossil Histeroidea are pictured in Figure 6. In the following paragraphs, I discuss some of the interesting fossils more in depth.
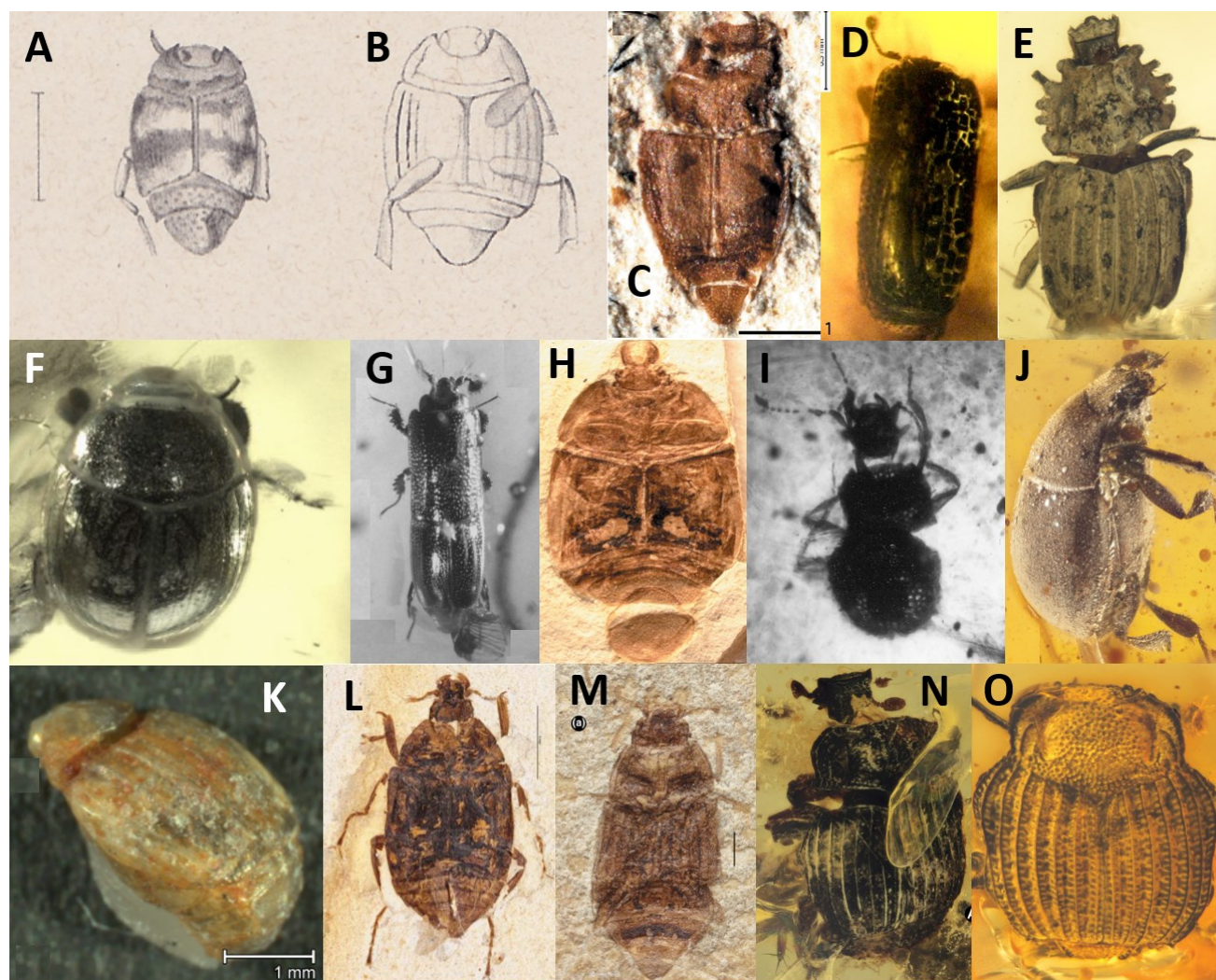
Figure 6. Examples of known Histeroidea fossils. A – *Hister maculigerus*, B – *Hister antiquus*, C – *Plegaderus pitoni*, D – *Carcinops donelaitisi*, E – *Cretonthophilus tuberculatus*, F – *Xestipyge ikanti*, G – *Trypanaeus hispaniolus*, H – *Hister cerestensis*, I – *Pantostictus burmanicus*, J – *Yethiha peregrina*, K – *Onthophilus intermedius*, L – *Cretohister sinensis*, M – *Antigracilus costatus*, N – *Carinumerus yingae*, O – *Carinumerus maddisoni*. All figures adopted from following publications: Alekseev (2016), Caterino et al. (2015), Caterino (2021), Chatzimanolis et al. (2006), Degallier et al. (2019), Heer (1862), Jiang et al. (2020), Poinar & Brown (2009), Schwermann et al. (2016b), Zhou et al. (2018, 2020)

Table 3. List of described fossil species of the Histeroidea. A – amber inclusion, C – compression, Ca – phosphatized cast

Family	Subfamily	Species	Age (mya)	Deposit, fossil type	Reference
Synteliidae	-	*Syntelia sunwukong*	99	Burmese amber, A	Jiang & Wang (2021)
Cretohisteridae	-	*Cretohister sinensis*	125	Yixian Form., China, C	Zhou et al. (2018)
Histeridae	Antigracilinae	*Antigracilus costatus*	125	Yixian Form., China, C	Zhou et al. (2020)
Histeridae	Abraeinae	*Pantostictus burmanicus*	99	Burmese amber, A	Poinar & Brown (2009); Zhou et al. (2020)
Histeridae	Dendrophilinae	*Yethiha peregrina*	99	Burmese amber, A	Caterino (2021)
Histeridae	Dendrophilinae	*Druantia aeterna*	99	Burmese amber, A	Caterino (2021)
Histeridae	Haeteriinae	*Promyrmister kistneri*	99	Burmese amber, A	Zhou et al. (2019)
Histeridae	Onthophilinae	*Cretonthophilus tuberculatus*	99	Burmese amber, A	Caterino et al. (2015)
Histeridae	Onthophilinae	*Carinumerus yingae*	99	Burmese amber, A	Jiang et al. (2020), (Caterino 2021)
Histeridae	Onthophilinae	*Carinumerus maddisoni*	99	Burmese amber, A	Caterino (2021)
Histeridae	Onthophilinae	*Phasmister cristatus*	99	Burmese amber, A	Caterino (2021)
Histeridae	?	*Amplectister tenax*	99	Burmese amber, A	Caterino & Maddison (2018)
Histeridae	Dendrophilinae	*Carcinops donelaitisi*	55,8-33,9	Baltic amber, A	Alekseev (2016)
Histeridae	Dendrophilinae	*Xestipyge ikanti*	55,8-33,9	Baltic amber, A	Alekseev (2016)
Histeridae	Dendrophilinae	*Bacanius kirejtshuki*	55,8-33,9	Baltic amber, A	Sokolov & Perkovsky (2020)
Histeridae	Dendrophilinae	*Bacanius goorskii*	55,8-33,9	Baltic amber, A	Alekseev & Bukejs (2021)
Histeridae	Onthophilinae	*Onthophilus intermedius*	45-25	Quercy, France, Ca	Handschin (1944)
Histeridae	Histerinae	*Hister cerestensis*	33,9-28,1	Céreste, France, C	Degallier et al. (2019)
Histeridae	Abraeinae	*Trypanaeus hispaniolus*	20,43-15,97	Dominican amber, A	Chatzimanolis et al. (2006)
Histeridae	Histerinae	*Hister aemulus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister antiquus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister coprolithorum*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister maculigerus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister marmoratus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister mastodontis*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister morosus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Histerinae	*Hister vetustus*	23-5,3	Oeningen, Germany, C	Heer (1862)
Histeridae	Abraeinae	*Plegaderus pitoni*	2,5-1,8	Lak Chambon, France, C	Degallier et al. (2019); Piton & Théobald (1935)

3.1 Cretaceous period

Weyenbergh (1869) described *Hister relictus* from Jurassic deposits in Solnhofen, Germany, but the position of the fossil was later revised and the species was transferred to a new genus *Pseudotenebrio* in the family Tenebrionidae (Handlirsch 1906). Therefore, the oldest known histeroid fossils date back to the Cretaceous period. Most of the specimens come from Burmese amber deposits in Myanmar (ca. 99 mya). Two species have been described from compression fossils from the Yixian Formation in China (ca. 125 mya). There are currently 12 described species from the Cretaceous (see Table 3 for complete list of described fossil species of Histeroidea).

The oldest confirmed Histeroidea fossils come from deposits of Yixian Formation in China. The locality yielded two species thus far – *Cretohister sinensis* (Figure 6L) and *Antigracilus costatus* (Figure 6M), both preserved as compression fossils. Their age is estimated at 125 mya. *Cretohister* was assigned to a newly described family Cretohisteridae (Zhou et al. 2018). *Antigracilus* was placed in a newly described Histeridae subfamily – Antigracilinae (Zhou et al. 2020).

Figure 7. *Promyrmister kistneri*. Black arrow marks possible exudates. Adopted from Zhou et al. (2019)

The other Histeroidea fossils from the Cretaceous come from Burmese amber. Some of them bear interesting morphological adaptations indicating their specialized habitat preferences and they can be a clue for the reconstruction of the habitat shift evolution:

Zhou et al. (2019) described *Promyrmister kistneri* (Figure 7) and placed it within the Haeteriinae subfamily based on morphological characters. All extant species of this subfamily are strictly myrmecophilous or termitophilous. Based on that fact, the authors deduced that this species was an inquiline in ant nests. The presence of gland openings and globules of possible exudates close to theirexpected positions supports this theory (Zhou et al. 2019). According to Barden & Grimaldi (2016) the earliest definitive eusocial ants already existed in the Upper Cretaceous. I would add that the beetle might have been a guest in the nests of termites whose eusociality developed significantly earlier – ca. 150 mya (Chouvenc et al. 2021).

Amplectister tenax (Figure 8) is a strange clown beetle with possible adaptations for inquilinism. The species possesses a strong ventral concavity with setae and enlarged grasping hind legs (Figure 8B). The authors hypothesised about the function of these modifications. Mate holding was considered first, as ventral concavity serves for males to hold onto females during copulation in some extant species. However, in such cases, the concavity is never as strong, nor does it bear setae. Moreover, the concavity should copy the dorsal shape of the beetle, which is not the case in *Amplectister*. Grasping modifications may appear as an adaptation for phoresy. The species might have been a mammal

Figure 8. *Amplectister tenax*. A - dorsal view, B - ventral view, black arrow marks the ventral concavity. Adopted from Caterino & Maddison (2018)

or bird inquiline and used these modifications for clinging to fur or feathers. However, no such cases are known

in the extant histerid species. For this reason, the authors proposed that *Amplectister tenax* was a guest in colonies of social insects and clung to the bodies of host ants or termites (Caterino & Maddison 2018). This behaviour is known among extant species of Haeteriinae, some of which are of similar size (less than 1.5 mm) as *Amplectister* (Caterino & Dégallier 2007; von Beeren & Tishechkin 2017). *Amplectister* has not been placed in any subfamilies, but Zhou et al. (2020) suggest it is possibly related to Onthophilinae (the subfamily contains several myrmecophiles (Ohara & Nakane 1986)).

Interestingly, over 30 % of the known Cretaceous histerid species are members of the Onthophilinae subfamily, which only has a little over 80 extant species (less than 2 % of the extant Histeridae species diversity) (Mazur, 2011). In addition, Onthophilinae form a significant part of the undescribed specimens that I know about. No hypothesis explaining this pattern has been published. Here I present some possible explanations.

1. **Sorting bias:** The Burmese amber may be a biased source and is not relevant for evaluating insect diversity of Cretaceous period as a whole. The bias can be of two types:
    a. **Geographical/ecological:** The palaeoenvironment where the Burmese amber was deposited had the character of a coastal tropical rainforest in a river estuary (Salamon et al. 2019) and was located in Southeast Asia. If the Onthophilinae was species-rich in the tropic rainforests of Asia, their diversity could be overestimated by data from Burmese amber. However, the current distribution of the subfamily is largely non-tropical and non-Asian: *Onthophilus* (ca. 40 spp., which represents 50 % of subfamily diversity) can be found almost exclusively in the Holarctic region. *Epiechinus* (ca. 30 spp.) is mostly a tropical genus with highest species diversity in Africa. *Sculptura* (2 spp.), *Sigillium* (1 sp.), *Vuattouxinus* (1 sp.) and *Glymma* (1 sp.) are all lineages endemic to the Afrotropical realm. *Peploglyptus* (3 spp.) is distributed in the Americas and Malaysia (Mazur 2011). Therefore, it is unlikely that the Burmese amber would overestimate the diversity of Ontophilinae for geographical or ecological reasons.
    b. **Selective trapping:** Amber can be viewed as a type of insect trap and, as all artificial insect traps, is selective in the groups of insects that it captures (Solórzano Kraemer et al. 2015). The amber could therefore sort the Histeroidea species by various factors, for example their flight ability or association with resin producing trees. Generally, almost all histerids (including onthophilins) are good fliers (active transport is vital for exploiting ephemeral sources/habitats; cave dwelling and endogean species usually lost flight ability) (Beutel et al. 2016; pers. obs.). Extant Onthophilinae are typically associated with faeces, mammal burrows, social insect colonies, forest litter, etc. (Mazur 1973; Ohara & Nakane 1986; T. Lackner, pers. comm.). Only the onthophiline genus *Epiechinus* can be found in the subcortical space or on rotting wood (Kovarik 1994). The majority of extant species of Onthophilinae are hence not associated with living or dying (and hence resin-producing) trees. Other histerid groups (Platysomatini, Trypanaeini, Trypeticini etc.) are more typical for these habitats. Thus, the hypothesis that Cretaceous Onthophilinae diversity would be overestimated by capture bias seems improbable to me.
2. **Extinct diversity:** This hypothesis assumes that in the Cretaceous, the Onthophilinae was a much more species-rich group inhabiting various habitats. They represented a large part of the Histeridae diversity at that time, therefore their high proportion among Histeridae fossils is natural. Later other Histeridae lineages have become dominant and have outcompeted the Onthophilinae. Most Onthophilinae lineages have become extinct, with only few surviving today. Caterino (2021) rejects the close relationship

between any of the described Cretaceous species and the extant members of the Onthophilinae. The Cretaceous species might form an extinct monophyletic clade, but there is not enough data to confirm this hypothesis. They could also represent several early divergent lineages that have become extinct. Either way, this indicates that the Onthophilinae diversity was higher in the Cretaceous, with a wider range of habitats and regions inhabited in which extant onthophilines are not found today. I consider this hypothesis more likely than the provious ones.

Cretaceous deposits will undoubtedly provide other interesting fossils in the future. Over past two years, I was able to acquire 11 undescribed fossil species in Burmese amber (Figure 9). Three of them belong to the subfamily Onthophilinae (Figure 9E–G), one is probably a subcortical species from the Platysomatini (Histerinae) (Figure 9D), several belong to the Abraeinae (Figure 9A-C) and some are yet to be assigned to a subfamily. The Platysomatini species is particularly interesting, as it is the oldest Histerinae fossil and the oldest fossil with likely subcortical habitat preference. The inclusions have been scanned on microCT to better visualise their morphology (as it is difficult to observe under light microscope).
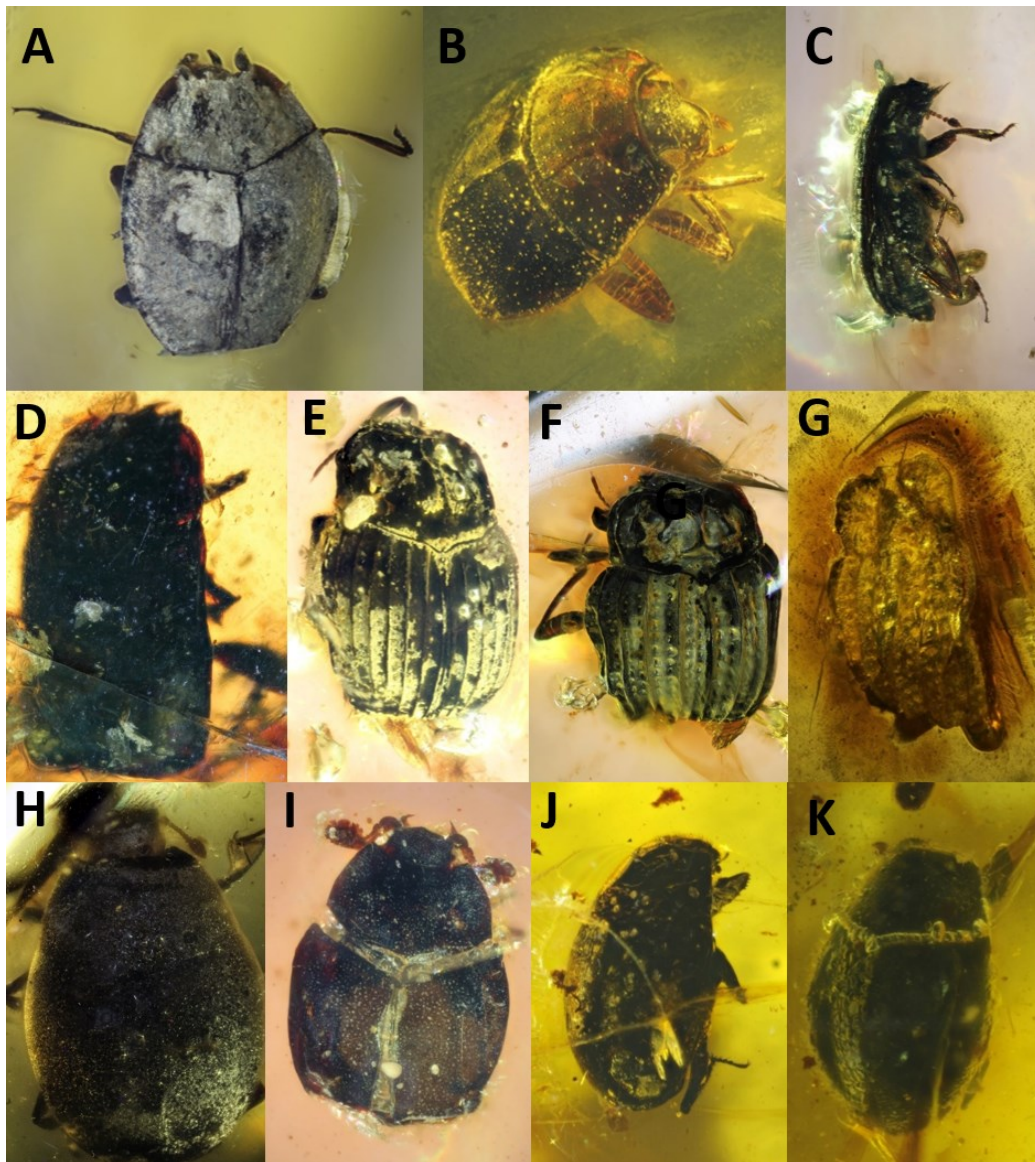

Figure 9. Undescribed Histeridae species from Burmese amber. A-C – cf. Abraeinae, D – Histerinae: Platysomatini, E-G – Onthophilinae, H-K – unassigned

3.2 Cenozoic fossils

Younger deposits have yielded several Histeridae fossils, mostly from the Eocene and Miocene periods. These fossils are interesting for documentation of Cenozoic diversity, but not that informative for phylogenetic studies because radiation of the main clades happened earlier (Zhou et al. 2020). However, they can still provide insights on habitat preference evolution.

Baltic amber is an important source of insect fossils from the Eocene period (Penney & Green 2010). Histeridae are also found in Baltic amber, but only four species have been described so far (Alekseev 2016; Alekseev & Bukejs 2021; Sokolov & Perkovsky 2020) (Figure 6D-E). Many others, including representatives of *Acritus*, *Abraeus*, *Platysoma*, *Hister*, *Bacanius*, *Carcinops* etc., have been reported from Baltic amber but not illustrated or described (Alekseev, 2016). Baltic amber hence remains an interesting source of fossil histerids and needs additional work and special attention.

Histerid compression fossils include *Hister cerestensis* (Figure 6G) from Oligocene deposits in Céreste, France (Degallier et al. 2019), *Plegaderus pitoni* (Figure 6C) from Pliocene deposits of Lak Chambon, France (Degallier et al. 2019; Piton & Théobald 1935), eight species of *Hister* (Figure 6A-B) from the Miocene deposit of Oeningen, on the border of Switzerland and Germany (Heer 1862). Another Miocene fossil was assigned to the extant *Margarinotus brunneus* by Schöberlin (1888). Chatzimanolis et al. (2006) disputed this identification and indicated that the fossil is an undescribed species.
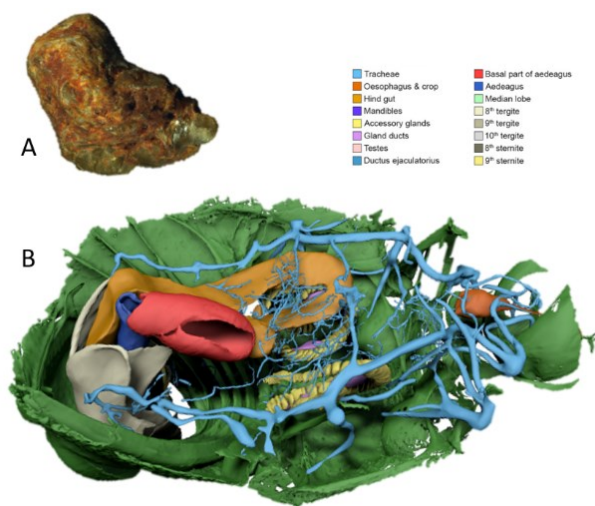
Figure 10 *Onthophilus intermedius*. A – original fossil, B – 3D model of the inner morphology. Adopted from Schwermann et al. (2016a)

Handschin, 1944 described *Onthophilus intermedius* (Figure 6I) from phosphorite deposits in Quercy, France from the Eocene-Oligocene period. The fossils are in the form of a mineralised cast of the beetle body. Recent studies (Schwermann et al. 2016a,b) revealed an amazing preservation of the inner morphology of these fossils (Figure 10). Even soft tissues were preserved and visualised using microCT.

Dominican amber is another source of well-preserved Miocene fossils. It also contains Histeridae inclusions, but only one species, *Trypanaeus hispaniolus* (Figure 1F), was described thus far (Chatzimanolis et al. 2006). Tishechkin (2007) mentions undescribed fossils of Haeteriinae in Dominican amber.

4   Ecology and life history strategies

Histeroid beetles can be found in various environments and habitats in all zoogeographical regions except Antarctica. Most species are predators, but adults in several lineages feed on fungal spores or microbiota coatings. Various histeroid lineages feed on a wide scale of prey species. Consequently, the diversity of habitat preferences within the group is extreme.

4.1   Immature stages and reproduction

Our knowledge of the immature stages of the Histeroidea remains limited. Larvae have two instars in all Histeridae (Kovarik 1995). In Synteliidae, the first and second larval instars as well as pupa have only been described for *Syntelia histeroides* (Mamaev 1974; Newton & Spangler 1991). Synteliidae apparently have only two larval instars, as in Histeridae (Beutel et al. 2016). In Sphaeritidae, only the first larval instar of *Sphaerites glabratus* has been reared and described (Hansen 1997; Newton & Spangler 1991; Nikitsky 1976).

The head capsule and the first thoracic tergite are strongly sclerotized in both instars of all Histeroidea (Figure 11). The rest of the body is membranous or weakly sclerotized (Newton & Spangler 1991); the sclerotization pattern does not vary much across the Histeroidea lineages (Beutel et al. 2016; Caterino & Tishechkin 2006; Kalashian 1995; Zaitsev & Zaitsev 2019). Larvae bear a pair of urogomphi, which are 2-segmented in Histeridae and 4-segmented in Sphaeritidae and Synteliidae (Beutel et al. 2016).

Figure 11. Larva of *Hister* sp. Photo by Giacomo Giovagnoli

Larvae of Histeridae, Synteliidae and Sphaeritidae are predaceous. They are liquid-feeders: they digest their prey extraorally and use all mouthparts and antennae tomanipulate it. The liquid is sucked by fast gut expansions and contractions working as a pump (Kovarik 1995). Larvae prefer to feed on prey with low mobility (Kovarik 1994).

Complete development (from egg to adult) has been documented to last from three to six weeks under ideal circumstances (Table 4). Temperature greatly affects the development duration, which can be more than doubled under poor conditions (Caneparo et al. 2017). Species that exploit ephemeral resources tend to have faster developmental rates than ones living in stable habitats (Kovarik 1994). The second larval instar ends with a phase called prepupa, which does not feed and usually constructs a pupal chamber. Some species (e.g., representatives of *Tribalus, Idolia, Hister, Saprinus* etc.) construct a cocoon. The cocoon is constructed from earth particles and lined from the inside with silk material emitted by the prepupa, which makes the walls very sturdy (Beutel et al. 2016; Kovarik 1994; Lindner 1967). Lindner (1967) observed that pupa could repair the cocoon if damaged. Adults can live for several years in some species (Beutel et al. 2016; Bornemissza 1968). In temperate areas, histerids usually overwinter as adults (Hinton 1945; pers. obs.).

Table 4. Duration of immature stages in Histeridae. Time in days, either as a mean or as a range provided by the studies. Sub. – subfamily, Abr. – Abraeinae, Trib. – Tribalinae, Hist. – Histerinae, Sapr. – Saprininae, Den. – Dendrophilinae; habitat – natural environment of the larvae; °C – temperature under which the development took place

Sub.	Species	Habitat	Egg	1st in.	2nd in.	Pupa	Total	°C	Reference
Abr.	*Teretriosoma nigrescens*	Subcortical	7	10	10	21	48	27	Rees (1985)
Trib.	*Epierus divisus*	Subcortical	10.75	10.5	14.16	10.5	45.91	25	Kovarik (1995)
Hist.	*Pachylister chinensis*	dung	2-3	16-20		21-35	39-58	25-30	Bornemissza (1968)
Hist.	*Hister coenosus*	dung/carrion	3.1	5.3	13.1	6.2	27.7	27	Summerlin et al. (1981)
Hist.	*Hister incertus*	dung/carrion	2.9	5.6	13.1	6.6	28.2	27	Summerlin et al. (1981)
Hist.	*Hister abbreviatus*	dung/carrion	2.8	4.2	9.6	12.6	29.2	27	Summerlin et al. (1984)
Hist.	*Hister unicolor*	dung/carrion	5	4-5	14	14-15	37-39	-	Lindner (1967)
Hist.	*Hister cadaverinus*	dung/carrion	6-7	7	14-16	14	41-44	23	Lindner (1967)
Hist.	*Margarinotus striola*	dung/carrion	4-5	4-5	14-16	12-14	34-40	20-25	Lindner (1967)
Hist.	*Margarinotus carbonarius*	dung/carrion	4-5	20-40		17-18	41-63	-	Lindner (1967)
Hist.	*Phelister panamensis*	dung	2.4	3	8.1	5.3	18.8	25-28	Summerlin et al. (1991)
Sapr.	*Saprinus semistriatus*	dung/carrion	4-5	5-6	12-13	12-13	33-37	-	Lindner (1967)
Sapr.	*Gnathoncus* sp.	carrion	6	5	13	16	40	-	Lindner (1967)
Sapr.	*Euspilotus assimilis*	dung/carrion	2.09	3.15	8.8	7.57	21.61	25	Kovarik (1995)
Sapr.	*Euspilotus azureus*	carrion	2.1	5.5	13.2	10.6	31.4	25	Caneparo et al. (2017)
Den.	*Carcinops pumilio*	poultry manure	3.5	3	8	6	20.5	30	Achiano & Giliomee (2005)

Reproduction. Some species (especially among Histerinae) perform simple courtship rituals. In many Histerinae species (*H. unicolor, H. cadaverinus, Spilodiscus floridanus* etc.) a male clings onto female's metatibia and follows the female as she moves around (Figure 12A). If she is willing to copulate with the male, she stops and allows him to mate. Otherwise, she keeps moving until the male eventually lets go (Beutel et al. 2016; Lindner 1967). Most Saprininae do not exhibit courtship behaviour, with the exception of *Xerosaprinus*. The eighth abdominal segment of males bears bristles. During courtship, this normally retracted segment is everted and moved back and forth, causing the bristles to vibrate. The vibrating bristles touch the female's head and pygidium for about 15 seconds; after several applications, the male attempts to mate with the female (Beutel et al. 2016). In *Epierus*, the male creates an elastic band prior to copulation, connecting his mouthparts and the female pygidium. The male then follows the female around before mating. When the distance between them increases, he is able to gather the tether and narrow the distance (Beutel et al. 2016). Males of *Plagiogramma* and *Epierus* possess setiferous tubercles or patches (Figure 12B), which are absent in females and probably play a courtship role. Males of some species bear morphological adaptations for easier positioning during copulation, such as ventral concavities on metasternum, copying the shape of female's pygidium in *Hister* etc. (Beutel et al. 2016; Lindner 1967).

After mating, females lay eggs individually and in small amounts, as they have only four ovarioles (Beutel et al. 2016; Lackner & Tarasov 2019; Summerlin et al. 1981, 1984). *Pachylister chinensis* oviposited two eggs per week on average (Bornemissza 1968). *Carcinops pumilio* oviposited up to six eggs within 24 hours for one to three days and then interrupted the oviposition for similar amount of time (Morgan et al. 1983). Eggs typically have an elongated shape and in some cases (e.g., in *Hister cadaverinus*) can be quite large, having the volume of over one third of the female's body (Hinton 1945).

Figure 12. Courtship in Histeridae. A – *Spilodiscus floridanus* male holding the female metatibia, B – setose patch on the head of the male of *Plagiogramma pubifrons*. Adopted from Beutel et al. (2016)

It seems that some histerids feature several traits typical for K-selected organisms – relatively small number of offspring, great longevity, large eggs and larvae etc. The latter may be explained by the fact that they feed on larval Diptera with typically rapid development. They must be of sufficient size in order to handle large prey. The presence of only two larval instars (in contrast with three in sister Hydrophiloidea (Beutel 1999; Newton & Spangler 1991)) may be caused by a similar selection pressure.

4.2 Diet

All Sphaeritidae, Synteliidae and the majority of Histeridae species are predaceous. Several histerid lineages have shifted to spore feeding but the vast majority of them have retained predaceous lifestyle. They prefer to feed on soft-bodied insect larvae or, less frequently, on eggs or pupae. Typically, these are Diptera larvae but immature stages of many other insect groups can serve as prey as well. Myrmecophile species feed on eggs and larvae of ants (Caterino & Dégallier 2007; Tishechkin 2007). The ants may also share their prey with them (Lenoir et al. 2012). Well-integrated myrmecophile species can even be fed with liquid produced by host ants (Akre 1968; Wheeler 1908). Dung associated histerids can consume scarabaeoid larvae in addition to maggots (Beutel et al. 2016). Psammophilous species prey on larvae of Diptera and tenebrionid or scarabaeid beetles (Beutel et al. 2016; Olexa 1990). Elongate subcortical species hunt for larvae or pupae of Scolytinae or Bostrychidae (Kanaar 2003; Mazur 1973). Some big tropical species prey on Curculionidae larvae (Beutel et al. 2016; Tresson et al. 2021). *Margarinotus scaber* eats larval Trogidae (Ramos et al. 2009). A small number of species consume larvae of Lepidoptera or Hymenoptera (Beutel et al. 2016). Some histerids actively search for prey on vegetation – *Hister helluo* preys on *Agelastica alni* larvae (Figure 15), *Saprinus virescens* hunts for *Phaedon armoraciae* (Bickhardt 1916; Yélamos 1989). Many species are capable of predating any soft-bodied insect larvae, eggs or pupae of appropriate size when offered (Kovarik 1994, pers. obs.). According to Lindner (1967), adults of *Margarinotus striola* can live and breed when fed only raw meat.

Adult insects: Histerids rarely feed on adult insects. Carlton et al. (1996) observed *Euspilotus bisignatus* feeding on adult Calliphoridae flies. The beetles probably stay hidden in faeces waiting for a fly to come to feed on the faeces liquid. *Euspilotus* consequently grasps the fly by its proboscis, continues to pierce the head capsule and eat its contents. The authors collected several bodies of flies around the dung, all of which had their head capsule hollow or partially hollow. The same authors reported an observation of *Psiloscelis opacus* capturing and feeding on adult ants. According to Aukema & Raffa (2004), *Platysoma cylindrica* invades the tunnels of *Ips pini*. Adult males and females of *Ips* protect the entrance to the egg chambers. When successful, *Platysoma* kills the adults and subsequently consumes them. Carvalho et al. (2020) observed *Hololepta reichii* consuming dead adults of stingless bees (although they preferred live larvae and pupae).

Other arthropods: The smallest representatives of Histeridae (*Acritus*, *Aeletes* etc.) sometimes feed on mites (Beutel et al. 2016). Another tiny histerid – *Halacritus instabilis* – hunts springtails (Prinz 1984).

Vertebrates: *Neopachylopus sulcifrons* is the only histerid known to prey on vertebrates. The species was found in the nests of the California grunion (*Leuresthes tenuis*). Following experiments proved that the species actively feeds on the fish's eggs (Thompson & Thompson 1919). Study by Olson (1950) discovered an association between the grunion nests and another histerid species – *Hypocaccus serrulatus* – but actual egg consumption was not observed in the study.

Sporophagy: Adults in several Histeridae lineages are sporophagous. They feed primarily on fungal spores but protist spores have also been found in their gut content (Kovarik 1994). Specialised sporophagous species have modified maxillary galea (Figure 13A), which bear setae serving as a comb for gathering spores (Beutel et al. 2016; Kovarik 1994; Newton & Spangler 1991). Interestingly, reproduction rate of these species is highest under conditions that are also ideal for fungi fructification (warmth, moist). Several nidicolous species of *Onthophilus* have small depressions on their mandibles that probably serve as mycangia (Kovarik 1994).

Primarily sporophagous taxa can be found in Tribalinae (*Epierus*, *Pseudepierus, Parepierus, Eutribalus, Idolia, Paridolia, Plagiogramma, Australepierus*), Dendrophilinae (*Cyclobacanius*, *Bacanius*) and Onthophilinae (*Epiechinus*). The guts of these taxa are often packed with spores. Several genera are probably facultative spore feeders (e.g., *Stictostix, Peploglyptus, Onthophilus*) (Kovarik 1994). Most sporophagous taxa are also capable of predating fly eggs and early instars. *Eutribalus* and *Paraepierus* have difficulty feeding on fly eggs and do not accept larvae at all. Their mouthparts are probably adapted for spore feeding to the extent that they are not effective for killing and consuming prey (Kovarik 1994). Larvae of sporophagous taxa are predatory as in other histerids (Kovarik 1994).

Filtrators: It seems that species of *Onthophilus* primarily filter particles of microbiota coating the surface of liquid on fresh dung. Their mandibles and maxillary galea bear special setae – a modification for spore feeding and filtering (Figure 13B). Species of *Onthophilus* also consume fly eggs or fungi spores (Beutel et al. 2016; Kovarik 1994).

Prey detection: Histeroids use chemical signals to locate the prey. These chemical signals can be volatiles from decomposing material, kairomones of prey (e.g., Scolytinae), volatiles of the prey's host plant, pheromones of social insects etc. (Beutel et al. 2016; Erbilgin & Raffa 2001a,b; Kovarik 1994). Antennae often bear complex sensory structures (Kovarik 1994; Lackner 2010) that probably enable histeroids to find prey or optimal habitats.
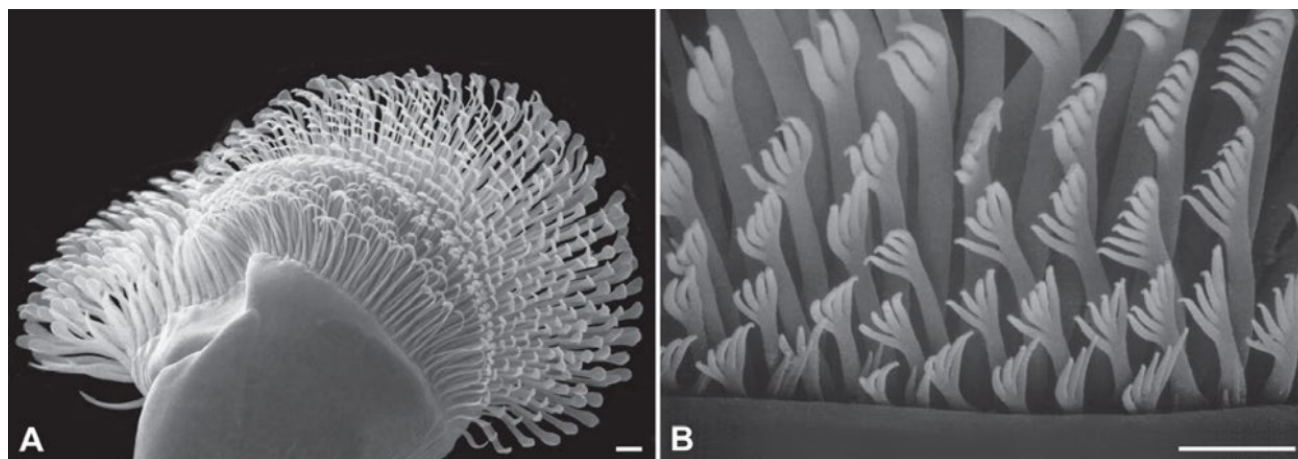

Figure 13. Mouthparts adaptations. A – *Epierus* sp. – maxillary galea with setae adapted for fungal spore gathering, B – *Onthophilus nodatus* – mandibular prosthecal filtering comb. Scale bars: 10 μm. Adopted from Beutel et al. (2016)

4.3   Habitats

As mentioned above, histeroids exploit a wide range of habitats and environments. Species vary from generalists that can be found in various places to extreme specialists, which live and breed only in very specific settings. Generally, histeroids can be found in places where their prey occurs. Larvae usually share same habitat with adults (Beutel et al. 2016; Caterino & Tishechkin 2006; Lindner 1967).

4.3.1   Decaying animal material

Animal faeces and carrion are a typical (micro)habitat where histerids can be found. The decaying material is an ideal substrate for the larval development of Diptera. Most histerids attracted to dung or carrion feed on Diptera larvae. Some also feed on the larvae of Scarabaeoidea, Trogidae etc.

Typical genera that can be found in dung or carrion are mainly representatives of the Histerinae and Saprininae subfamilies – *Hister, Margarinotus, Pactolinus, Pachylister, Atholus, Saprinus* etc., but species of small histerids of the subfamilies Abraeinae and Onthophilinae are attracted to dung as well (Beutel et al. 2016; pers. obs.). *Sphaerites* can also occur in dung (Wu & Sun 2012).

Figure 14. *Margarinotus scaber* and its habitat. Adopted from Verdugo Páez (2012)
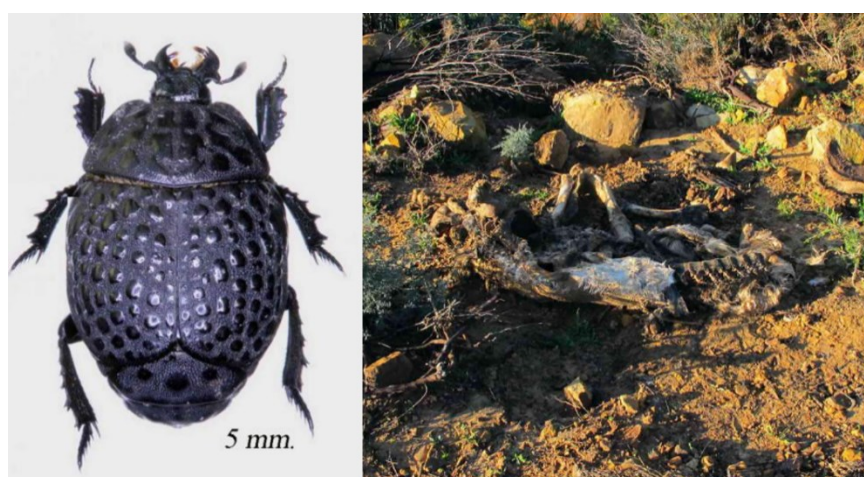
After faeces or carrion dry out most Diptera become absent. Larvae of insects able to exploit the left-over materials (keratin etc.) remain (Beutel et al. 2016). Some histerids are specialised in this later dry phase of decomposition. *Margarinotus scaber* (Figure 14, one of the most beautiful Histeridae species in my opinion) hunts larval *Trox* on dried carcasses (Ramos et al. 2009; Verdugo Páez 2012).

The majority of species attracted to dung and carrion live in an open, xerothermic environment with only a few exceptions (e.g., *Margarinotus striola succicola*, which is a forest species) (Lackner 2015). Dung-associated species may serve as predators of economically important pests, such as *Haematobia irritans* or *H. exigua* (Bornemissza 1968; Summerlin et al. 1991). Necrophilous species may be of importance to forensic entomology (Caneparo et al. 2017; Szelecz et al. 2018).

Interestingly, histerids are also attracted to blossoms of plants that mimic decaying carcasses to attract fly pollinators. They do not feed on any prey there and probably are only confused by the plants' volatiles (Beutel et al. 2016). Previous authors (Beutel et al. 2016; Reichardt 1941) propose they do not serve as pollinators as they often destroy the flowers.

4.3.2   Decaying plant material and live plants

Rotting vegetation is another common place for the development of histeroids' prey. Some species (e.g., *Atholus bimaculatus*, *Hister illigeri*) are generalists and live in composts as well as dung and other decomposing materials (Mazur 1973; Yélamos 1989, pers. obs.). Some species are known to regularly occur in forest litter (Beutel et al. 2016). Lackner (2010) reports some species found in debris under specific south Palearctic plants – *Exaesiopus atrovirens*, *E. torvus* and *Chivaenius kryzhanovskii* under *Tamarix* spp., *Saprinillus paromaloides*

and *S. kryzhanovskyi* under *Kalidium gracilis*. Tree cavities with organic material host numerous Histeridae species (e.g., *Abraeus* spp., *Acritus* spp., *Margarinotus merdarius*) (Beutel et al. 2016; Lackner 2015; pers. obs.). Some sporophagous species also live in decomposing wood where they feed on fungal spores (Kovarik 1994).

Rotting succulents: Rotting cacti (and other succulents) is an important source of both water and nutrients in desert areas of the Americas. Some histeroid species are specialised purely in this habitat and their larvae will only develop there. *Syntelia westwoodi* finds prey in big rotting pillar cacti in the high altitude Mexican desert (Bravo-Avilez et al. 2019; Sallé 1873; A. Newton pers comm.). Several *Hololepta* and *Omalodes* species are found in association with various species of rotting Cactaceae, Agaveae etc. In the old world, *Euphorbia* species represent an equivalent habitat, inhabited by a number of histerid species (e.g., *Atholus euphorbiae*, *Afrosoma castanipes*) (Beutel et al. 2016; Yélamos 1993). *Paravolvulus syphax* develops in drying and decaying stalks of *Cistanche* plants (Kryzhanovskij 1987; Kryzhanovskij & Reichardt 1976).

Living plants: Several Neotropical histerids (e.g., species of *Hololepta, Oxysternus, Carcinops*) are associated with palms, where they prey on weevil larvae (Beutel et al. 2016; Reichardt 1941). *Plaesius javanus*, *Hololepta quadridentata* and *Hister niloticus* are predators of an important banana and sugar cane pest – weevil *Cosmopolites sordidus* – and have been considered as a potential tool for its biological control (Tresson et al. 2021). *Baconia batula* is associated with bamboo (Caterino & Tishechkin 2013a). Cycads host several histerid species (e.g., *Platysoma conditum*, *Pachycraerus chalybeum*), which feed on larval Lepidoptera,

Figure 15. *Hister helluo* preying on Chrysomelidae larvae. Photo from insectarium.net

Coleoptera and Hymenoptera developing in the plant (Beutel et al. 2016; Yélamos & Kanaar 1997). *Hister helluo* (Figure 15) and *Saprinus virescens* actively run on vegetation in pursuit of their prey – Chrysomelidae larvae (Bickhardt 1916).

Roots: Some species live around plant roots. Rotting roots of *Ferula* (Apiaceae) in Southern Palearctic attract *Atholus rudesculptus, Chaetabraeus subconvexus, Hister turanus, Margarinotus oblongulus,* and *M. bueckingi* (Kryzhanovskij & Reichardt 1976; Olexa 1982). South Palearctic species *Atholus astragali, A. khnzoriani, A. siculus*, and *Platylister simeani* are attracted to decaying roots of *Astragalus* (Fabaceae) (Olexa 1987). *Atholus siculus, Hister semenovi, Margarinotus oblongulus, Atholus holzschuhi* and *A. Peloponnesus* have also been reported in association with various plant roots (Beutel et al. 2016; Olexa 1982). Many psammophilous species live near rhizosphere of Poaceae and other plants (Lackner et al. 2019, pers. obs.).

Blossoms: Only few species have been recorded in flowering plants. Several species of *Hololepta* and *Omalodes* have been collected from inflorescenses of South American *Heliconia bihai* (Musaceae). *Carcinops schwarzi* was reported from the flowers of *Attalea* palms (Beutel et al. 2016). Several species of *Saprinus* are attracted to flowers mimicking rotting meat (Reichardt 1941).

Fermenting fruit: Some histerids (e.g., *Hololepta*, *Omalodes*) are attracted to rotting fruit (Moura & Almeida 2013; Siepmann 1932).

4.3.3 Decaying fungi material

Some species of *Notodoma*, *Baconia*, *Epitoxus*, *Hister*, *Margarinotus*, *Saprinus* (and other genera) prey on larvae in rotting fungi (Beutel et al. 2016; Lackner 2010). *Sphaerites* is also commonly found in association with rotting fungi (Beutel et al. 2016). In most cases these interactions are not obligatory, rather the species are generalists that can also be found on other substrates (Beutel et al. 2016; Lackner 2010; Mazur 1973; Reichardt 1941). For example, *Sphaerites* is also found in dung, carrions, fermenting fruit or in association with sap of dying trees (Lackner 2015; Mazur 1973; Wu & Sun 2012). Specialised fungi species include *Notodoma* spp., *Baconia chujoi*, *Hister fungicola*, *H. indistinctus*, *H. defectus*, *Margarinotus lecontei*, *Operclipygus* spp. (Beutel et al. 2016; Caterino 1999; Caterino & Tishechkin 2013b).

4.3.4 Subcortical space

Space under the bark of dead or dying trees is an environment with rich biodiversity and high abundance of various arthropods and other invertebrates. The space retains moisture while decomposing phloem, cambium, wood, bark and fungi growing there all serve as bountiful food source (Birkemoe et al. 2018). Many species of Histeroidea have specialised in inhabiting the subcortical space and prey on invertebrates there.

Most subcortical histeroids can be divided into two morphotype groups – dorsoventrally flattened species and cylindrical ones.

Flat body shape: Most species of the tribe Hololeptini are (often extremely) flattened (although some inhabit different habitats – they tend to be rather slightly flattened) (Figure 16). Flat taxa can also be found among representatives of the histerine tribes Platysomatini (*Platysoma*, *Placodister*, *Eblisia*) and Exosternini (*Pachycraeurus*, *Macrosternus*, *Grammopeplus*, *Hypobletus*). Some Dendrophilinae are also flattened due to subcortical life – these include species of *Platylomalus*, *Pachylomalus*, *Carcinops*.
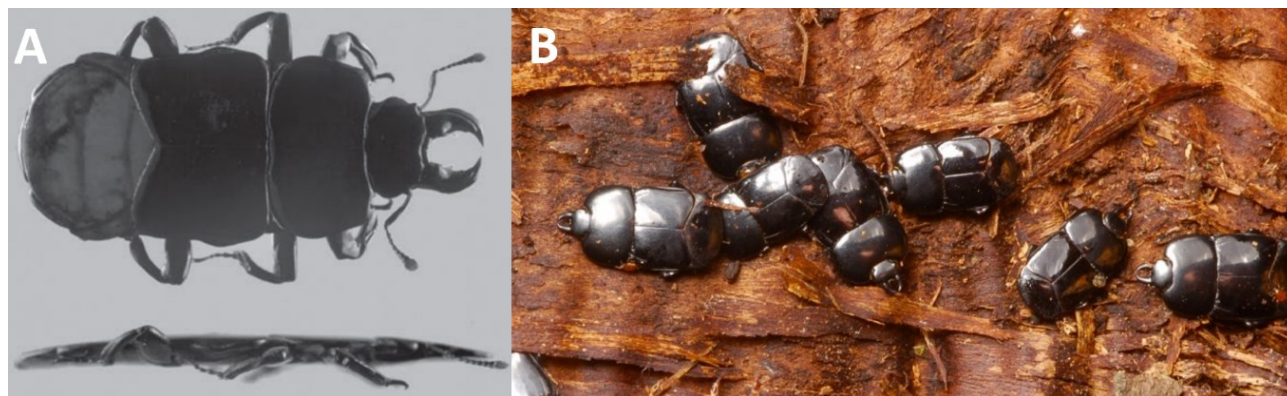
Figure 16. Flattened morphotype. A – Hololepini sp. – dorsal and lateral view (adopted from Beutel et al. (2016)); B – *Hololepta plana* in its habitat (photo by Marek W. Kozłowski)

Cylindrical body shape allows histeroids to move through the tunnels of wood-boring insects (Scolytinae, Bostrychidae etc.), upon whose larvae they feed (Beutel et al. 2016; Kanaar 2003; Zaitsev & Zaitsev 2019). Several big Histeridae lineages possess this body shape. These include: Niponiinae (Asian in distribution, Figure 17B), Trypanaeini (Neotropical, Figure 17C), Trypeticini (Oriental-Australian, Figure 17D) (Beutel et al. 2016; Mazur 2011). Cylindrical morphotypes can also be found in some species of *Teretrius* (Abraeinae, Figure 17E), *Platysoma* (Histerinae) and others (Beutel et al. 2016; Lackner 2015). All Synteliidae (Figure 17A) also bear

a cylindrical shape and, with the exception of *Syntelia westwoodi,* they are all found in the subcortical space of fallen trees in high altitudes (Beutel et al. 2016).
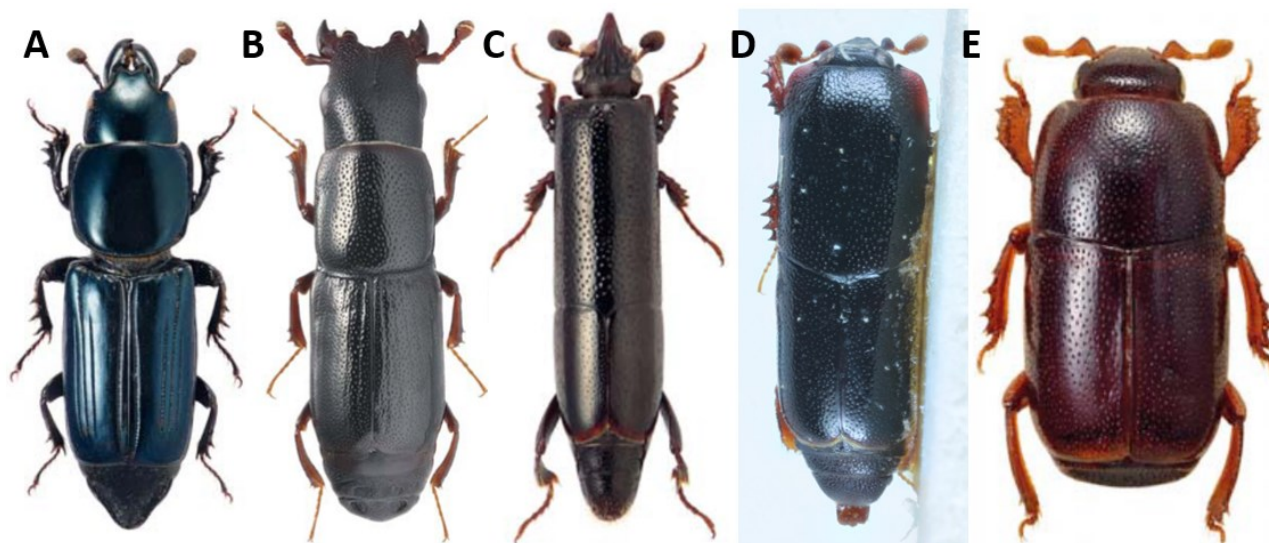
Figure 17 Species with cylindrical body shape; A – *Syntelia mazuri* (Synteliidae), B – *Niponius osorioceps* (Histeridae: Niponiinae), D – *Trypeticus cinctipygus* (Histeridae: Abraeinae: Trypeticini), E – *Teretrius fabricii* (Abraeinae). Adopted from Lackner (2015) and Zaitsev & Zaitsev (2019)

Minute Histeridae that inhabit the subcortical space are usually only slightly flattened or/and elongate. It seems that due to their size they can move freely in narrow or tight spaces. Minute subcortical Histeridae include species of *Plegaderus* (Abraeinae), *Paromalus* (Dendrophilinae), *Epiechinus* (Onthophilinae) etc. and they prey on various tiny arthropods (Beutel et al. 2016; Mazur 1973). Some small subcortical histerids (e.g., species of *Epierus, Epiechinus*) feed on fungal spores (Kovarik 1994).

4.3.5 Social insect inquilinism

Social insect inquilinism has played an important role in Histeridae evolution. It includes groups associated with ants (myrmecophilous) or termites (termitophilous). The termite eusociality is about 150 million years old (Chouvenc et al. 2021) while the first eusocial ants were found in Burmese amber dating to ca. 99 million years ago (Barden & Grimaldi 2016). Apparently, some histerid lineages adapted to myrmecophily very early after the origin of ant eusociality. *Promyrmister kistneri* is the first supposed myrmecophile fossil of all insects, also dating back to 99 mya (Zhou et al. 2019) – see chapter 3.1 for more information about the species.

Histeridae contain two monophyletic species-rich subfamilies that are exclusively myrmeco- or termitophilous – Haeteriinae and Chlamydopsinae. They are well-integrated guests and interact with the ants often (e.g., ants carry them, feed them, they groom each other etc.). They usually cannot breed and survive long term outside of their host colony (Kistner 1982). Most species are probably host specific (Beutel et al. 2016) while several have been found with multiple species of ants, in some cases even with species from several different ant subfamilies (Caterino & Dégallier 2007). They have evolved a diverse morphology, often very bizarre and different from the other Histeridae forms (Figure 18). I discuss their adaptations in following paragraphs. We can find ant and termite inquilines in all other extant subfamilies, with the exception of Niponiinae (Tishechkin 2007), but usually they are rather unwelcomed or ignored guests who avoid contact with the ants (Beutel et al. 2016). Representatives of these subfamilies with social insect associations are listed below. Synteliidae and Sphaeritidae do not occur in social insect nests.

Haeteriinae is a diverse group both by number of taxa and morphological diversity. The subfamily contains little over 330 described species in more than 110 genera (Beutel et al. 2016). Tishechkin (2007) noted that 65 % of haeteriine genera are monotypic and only 8 % of them have more than four species. He pointed out that Haeteriinae is one of the most diverse, exclusively inquilinous, monophyletic lineages among all insects. The subfamily has very diverse morphology, including taxa that are spiky (e.g., *Symphilister*), setose (e.g., *Microsynodites*), elongate (e.g., *Thaumataerius*) or dorsoventrally flattened (e.g., *Euxenister*) (Helava et al. 1985; Tishechkin 2007).

The vast majority of the group's diversity can be found in the Neotropics. Nearctic realm is home to most species of following genera: *Haeterius*, *Pinaxister, Renclasea*, as well as several *Terapus* spp.*, Aritaerius pallidus, Ulkeus intricatus,* and *Hippeutister californicus*. Palearctics have all the species of *Satrapes, Eretmotus* and *Sternocoelis,* mostly distributed in North Africa and southern Europe, and a small of number of *Haeterius* species, two of them reaching as far east as Japan (Mazur 2011).

Termite host species include representatives of Nasutitermitinae and Termitinae. Ant host species (which are more frequent hosts than termites) include especially ecitonine army ants but also Myrmicinae and Ponerinae in the Neotropics, while Dolichoderinae, Formicinae, and Myrmicinae are their hosts in the rest of the world (Beutel et al. 2016).

Interestingly *Scapicoelis tibialis* has probably abandoned the myrmecophilous lifestyle. Numerous adults have been reared from a spider egg sac (Kapler 1999) and an adult has been observed on low vegetation (Degallier 1979).

Chlamydopsiinae are almost purely Australasian. Several species also live in Indonesia, Philippines, Japan, Malaysia, Vietnam, Taiwan and India (Mazur 2011). Information about host associations is only available for a limited number of species as many have only been collected in flight intercept traps while migrating between colonies (A. Tishechkin, pers. comm.). They have been found in nests of Myrmicinae, Ponerinae, Dolichoderinae and Formicinae ants. One species has been reported from the nests of *Eutermes* termite (Caterino & Dégallier 2007).

Representatives of the subfamily often bear bizarre morphological adaptations, which may include elongate legs (Figure 18A), gland openings, elytral trichomes (Figure 18B-C) etc. The beetles have also lost body pigmentation. Elongate legs apparently serve for grasping to the host for phoresy (Caterino & Dégallier 2007).
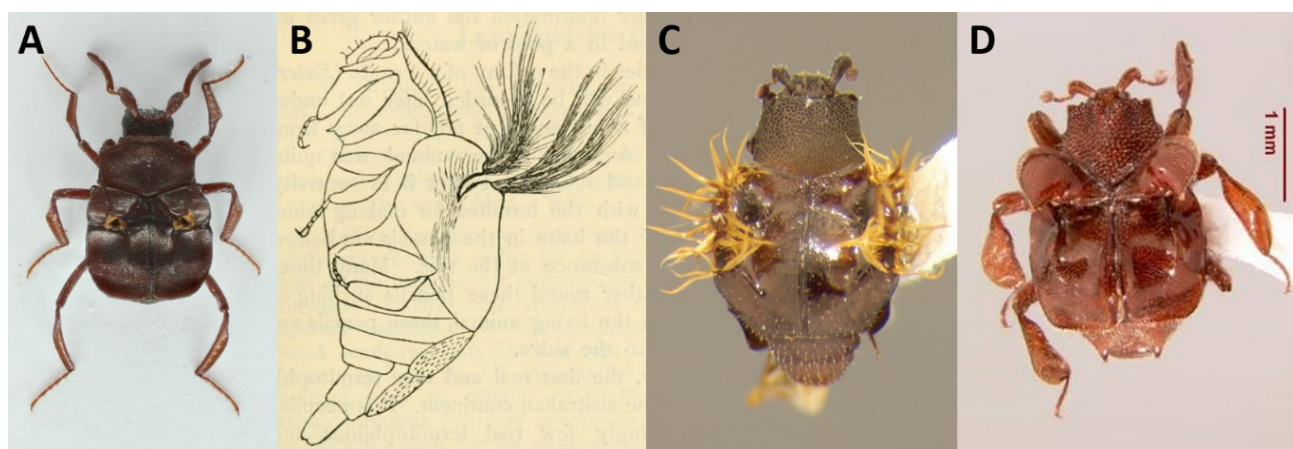

Figure 18. Chlamydopsinae. A – *Chlamydopsis dispersa*, B – *Eucurtia comata*, C – *Chlamydonia erectopilosa*, D – *Eucurtiopsis avis*. Adopted from Caterino (2006), Mjöberg (1912), Tishechkin & Caterino (2007)

Feeding habits: Both Haeteriinae and Chlamydopsinae are well-integrated in the colonies. They usually feed on the host's brood (Caterino & Dégallier 2007; Helava et al. 1985), although several species have been observed being fed with liquid by the ants (Akre 1968; Wheeler 1908). Ants may also share their prey with them (Lenoir et al. 2012).

Protective adaptations: Inquiline beetles have evolved various adaptations to stay safe. Enlarged scape covers the antennal club when the antenna is retracted (Helava et al. 1985). Other body appendages are also typically well protected when retracted (Akre 1968). Chemical signals play an important role as well. Haeteriinae have chemical glands that produce volatiles that probably attract or relax the ants (Akre 1968; Kistner 1982). The elongate hairs of *Eucurtia comata* serve for disseminating substances attractive to the host (Caterino & Dégallier 2007; Mjöberg 1912). Several Chlamydopsinae species can be found in nests of multiple ant subfamilies, suggesting the beetles are capable of obtaining chemical camouflage from the host species (Caterino & Dégallier 2007). Some Haeteriinae species have tibial grooms that probably serve for gathering the colony's odour, while riding on the ants (Kistner 1982). Reciprocal grooming between ants and beetles takes place in several Haeteriinae (Akre 1968).

Transport: As mentioned above, the Neotropical haeterines are typically associated with ecitonine army ants. Migration with the colony presents a challenge to the inquilines and they have evolved multiple solutions. Some Haeterines simply walk (Akre 1968). Several have been observed following the pheromone trail after the colony passed (Beutel et al. 2016). Apparently, long legs can serve for effective movement, as in the case of nidicolous or troglobiotic histerids (Kistner 1982). Phoresy is also common. Beetles have evolved various structures (costae, expanded tibiae etc.) that serve as handles for ants to carry them (Beutel et al. 2016). Several species are able to cling onto the beetles with their legs or mandibles (Akre 1968; von Beeren & Tishechkin 2017). Long legs are an adaptation for phoresy (Caterino & Dégallier 2007). Phoresy is also found in guests of non-migrating ants (Lenoir et al. 2012). When migration between colonies occurs, it is performed by flight, which is why both haeterines and chlamydopsines are often collected in flight intercept traps (A. Tishechkin, pers. comm.).

Histerinae contain many myrmecophilous and termitophilous lineages, mostly falling in the para/polyphyletic Exosternini. Species of *Paratropus* live in symbiosis with Dorylinae ants or in abandoned termite nests (Kanaar 1997). All *Coelocraera* spp. are associated with *Dorylus* ants (Kistner 1982). Other inquiline histerines include representatives of *Hister* spp. (with *Atta* and *Acromyrmex* ants), *Phelister* spp. (with *Atta* and Ecitoninae ants, *Nasutitermes* spp.), *Operclipygus* spp. (with *Atta*, *Acromyrmex* and Ecitoninae ants, *Nasutitermes* spp.), *Epiglyptus costatus* (with *Atta* ants), *Kaszabister* (with *Solenopsis* ants), *Psiloscelis* spp. (with *Formica* ants, one species has even been observed to feed on adult ants), *Mecistostethus pilifer* (with *Pachycondyla striata*), *Arbolister termitophilus* (with *Nasutitermes graveolus)*, and *Sitalia severini* (with *Odontotermes obesus*) (Beutel et al. 2016; Carlton et al. 1996; Caterino & Tishechkin 2013b; Caterino et al. 2012; Dégallier et al. 2012; Hinton 1935; Navarrete-Heredia 2001).

Saprininae: Myrmecophilous Saprininae include Palearctic *Myrmetes paykulli* (with *Formica*), South American *Phoxonotus* spp. (with *Atta*), *Euspilotus* (*Platysaprinus*) spp. (with *Acromyrmex* and *Atta*), *Paramyrmetes foveipennis* (with *Pogonomyrmex serpens*), North American *Geomysaprinus* sp. (with *Atta texana*) and Australian *Iridoprinus myrmecophilus* (with *Iridomyrmex purpureus*) (Hinton 1935; Lackner 2014a, 2017; Lackner & Leschen 2017). Kistner (1982) reported an association between some species of *Hypocacculus* and Dorylinae ants. Some saprinines are also termitophilous. These include the Australian

Saprinus rarus (with *Nasutitermites walkeri*), the African *Nannolepidius braunsi* (with *Hodotermes*) and the African *Pilisaprinus verschuneri* (in abandoned nests of *Macrotermes*) (Lackner & Leschen 2017).

Abraeinae: Several *Abraeus* and *Acritus* species have been reported from *Atta* colonies. *Aeletes termitophilus* was collected from nests of *Coptotermes niger* (Beutel et al. 2016; Wenzel 1944). Several European abraeines (e.g., *Abraeus parvulus*, *A. perpusillus*) are often found in association with *Lasius* or *Campanotus* ants but rather than inquilinism this is an example of niche sharing (Lackner 2015; Mazur 1973).

Dendrophilinae myrmecophiles are *Carcinops* spp. (with *Atta* ants), *Xestipyge multistriatum* (with *Atta* ants) and *Dendrophilus pygmaeus* (with *Formica* ants) (Bickhardt 1916; Kanaar 1999; Navarrete-Heredia 2001). The inquilinism is not always obligatory (Mazur 1973).

Onthophilinae also have only few myrmecophiles: the East Asian *Onthophilus silvae* lives in colonies of *Lasius* ants (Ohara 1999). *Onthophilus leconti* (primarily mammal inquiline) and another *Onthophilus* species have been reported from nests of *Pogomyrmex* ants (MacKay 1983). *Sculptura kivuensis* lives in nests of *Myrmicaria* ants (Kovarik 1994).

Tribalinae: Several species of tribaline *Plagiogramma* have been collected from nests of *Atta* ants. *Kissister minimus* and *Tribalus maroccanus* have a weak association with *Pheidole* ants in Spain and Morocco (Beutel et al. 2016; Hinton 1935).

Bees (Apidae) may be associated with some histerids. *Euspilotus pipitzi* has been collected in the nest of *Trigona rufictus* (Mazur 1974). *Hololepta reichii* have been repeatedly reported from nests of *Melipona* spp. and *Apis mellifera* (Carvalho et al. 2020; Coletto-Silva & Freire 2006). *Omalodes foveola* has also been found in honey bee hives (Krüger et al. 2017).

4.3.6 Vertebrate inquilinism

Many Histeridae species are associated with vertebrate nests or with the burrows of mammals, birds and in few cases also reptiles. Adult beetles are attracted to faeces deposited in the burrow or nest and feed on fly larvae there (Beutel et al. 2016). Nidicolous Onthophilinae often feed on microbiotic films on wet faeces. Some of them are also sporophagous. Several even have small depressions on mandibles that possibly serve as mycangia (Kovarik 1994). Some species require this environment for successful breeding, while others are occasional visitors that also proliferate elsewhere (Beutel et al. 2016; Kovarik 1994). In some cases many generations may live in one burrow without leaving it (Kovarik 1994). The majority of nidicolous species belong to Histerinae, Saprininae and Onthophilinae, but the subfamilies Abraeinae and Dendrophilinae also have several taxa that have been collected from these microhabitats. According to Beutel et al. (2016), many of the nidicolous Histeridae species share morphological features such as elongate legs and antennae, similar to the cave-dwelling species. Kovarik & Skelley (2019) suppose that elongate legs of the cave-dwelling species enable these beetles to move quickly through long underground systems and Kovarik (1994) provided the same explanation for nidicolous onthophilines. Histeridae inquilines can serve as effective predators of birds' or mammals' parasites and therefore may be beneficial to their hosts (Lundyshev & Tishechkin 2013).

Mammal burrows: Most nidicolous histerids are associated with mammals and are particularly specialised to rodent burrows.

Common hosts include Palearctic and Nearctic ground squirrels (*Spermophilus* spp., *Xerospermophilus*, *Spermophilopsis* spp.), North American prairie dogs (*Cenomys* spp.) and marmots (*Marmotta* spp.).

Nearctic gophers (Geomyidae, namely genera *Geomys*, *Thomomys* and *Cratogeomys*) host a particularly rich diversity of obligatory nidicolous histerids. Beutel et al. (2016) explain that gophers close their entrances during daytime. This access restriction has led to a higher fidelity of the inquilines. Some of the species produce a strong odour when handled (Beutel et al. 2016), which is an uncommon trait in Histeridae. This has not been explained, antipredatory adaptation seems unlikely, as pocket gophers are strictly herbivorous.

Other rodents that host Histeridae include gerbils (*Meriones* spp.), hamsters (*Cricetus cricetus*, *Cricetulus* spp.), long-clawed mole-voles (*Prometheomys schaposchnikowi*), flying squirrels (*Glaucomys* spp.), tuco tucos (*Ctenomys* spp.), kangaroo rats (*Dipodomys* spp.), jerboas (*Jaculus* spp.), voles (*Microtus* spp.), mice (*Mus* spp), packrats (*Neotoma* spp.) and African mole-rats (*Tachyoryctes* spp.).

Some Histeridae have also been found in the burrows of pikas (*Ochotona* spp.), rabbits (*Oryctolagus cuniculus*), European moles (*Talpa europaea*) and European badgers (*Meles meles*). The known associations of Histeridae with mammals are summarized in Table 5.

Table 5. Histeridae associated with mammals. [1] true nidicolous species found (almost) only in burrows of the specific mammal taxa, [2] true nidicolous species that are commonly found in burrows/nests of other mammal or bird taxa as well, [3] occasional visitors of burrows, [x/y] both options are found within the taxon, [x/y?] status uncertain

Mammal host	Histeridae guest species	Reference
Spermophilus spp. *Xerospermophilus* spp.	*Margarinotus pluto*[2], *M. hailar*[2], *M. ephemeralis*[1], *M. remotus*[1], *Dendrophilus sulcatus*[3], *D. proditor*[2/3?], *Gnathoncus disjunctus suturifer*[2], *G. kiritchenkoi*[2], *Geomysaprinus suffusus*[2], *G. saulnieri*[2], almost all *Pholioxenus* spp.[1/2], *Chalcionellus decemstriatus*[3], *Saprinus turcomanicus*[?], *Hypocaccus hungaricus*[1], *Onthophilus punctatus*[2], *O. lecontei*[2], *Aphelosternus interstitialis*[1], *Microsaprinus therondianus*[2], *Spilodiscus ulkei*[3], several *Geomysaprinus* spp.[1/2]	Beutel et al. (2016), Caterino (1998), Ivanov (2000) as cited in Beutel et al. (2016), Kovarik et al. (1999), Kryzhanovskij (1977), Kryzhanovskij & Reichardt (1976), Lackner (2010), Lackner & Seres (2018), Mazur (1973), Reichardt (1941)
Spermophilopsis spp.	*Gnathoncus kiritchenkoi*[2], *Erebidus vlasovi*[2], *Pholioxenus orichalceus*[2]	Kryzhanovskij (1977), Reichardt (1941)
Cynomys spp.	*Phelister warneri*[1], *Onthophilus cynomysi*[1], *Saprinus discoidalis*[?]	Beutel et al. (2016), Caterino & Tishechkin (2019), Helava (1978) as cited in Beutel et al. (2016), Kovarik & Skelley (2019)
Marmota spp.	*Margarinotus egregius*[3], *M. pluto*[2], *M hailar*[3], *Xestipyge puncticulatum*[3], *Gnathoncus disjunctus suturifer*[2], *Dendrophilus proditor*[2/3?], *Geomysaprinus obsidianus*[3]	Beutel et al. (2016), Caterino (2010), Chehlarov et al. (2016), Kryzhanovskij (1977), Reichardt (1941)
Geomys spp.	*Margarinotus felipae*[1/3?], *Atholus minutus*[1], *Atholus nubilus*[3], *Spilodiscus gloveri*[1], *S. floridanus*[1/3?], *S. flohri*[1], *Geomysaprinus rugosifrons*[1], *G. goffi*[1], *G. tibialis*[1], *Onthophilus kirni*[1], *O. giganteus*[1], *O. wenzeli*[1], *O. burkei*[1], *Phelister mobilensis*[3], *P. subrotundus*[3]	Beutel et al. (2016), Blume & Summerlin (1988), Caterino (1998), Caterino & Tishechkin (2019), Connior et al. (2014), Hubbell & Goff (1939), Kovarik & Skelley (2019), Ross (1940, 1944a,b), Skelley & Kovarik (2001)
Orthogeomys spp.	*Operclipygus bidessois*[3]	Caterino & Tishechkin (2013b)
Thomomys spp.	*Geomysaprinus saulnieri*[2], *G. paeminosus*[1/2?], *G. obscurus*[2], *Eremosaprinus baja*[1/2/3?] *Onthophilus lecontei*[2], *O. thomomysi*[1], *O. soltaui*[1], *Margarinotus thomomysi*[1]	Beutel et al. (2016), Caterino (2010), Helava (1978) as cited in Beutel et al. (2016), Kovarik et al. (1999), Ross (1952)
Cratogeomys merriami	*Onthophilus reyesi*[1]	Kryzhanovskij (1992)
Jaculus spp.	*Pholioxenus quedentfeldti*[2], *P. schatzmayri*[2]	Beutel et al. (2016), Kryzhanovskij (1977), Reichardt (1941)
Dipodomys spp.	Almost all North American *Eremosaprinus* spp.[1/2], *Geomysaprinus suffusus*[2], *Phelister brevistriatus*[3]	Beutel et al. (2016), Caterino & Tishechkin (2019), Wenzel (1939)

Mammal host	Histeridae guest species	Reference
Ctenomys spp.	*Euspilotus* spp.[1/2/3], *Paraeuspilotus monte*[1], *Aeletes ctenomyphilus*[1], *Pseudister* spp.[1/2/3], *Operclipygus latemarginatus*[3], *Phelister bruchi*[1], *P. nidicola*[1]	Arriagada & Aballay (2020), Beutel et al. (2016), Bickhardt (1920), Caterino & Tishechkin (2013b)
Glaucomys spp.	*Dendrophilus xavieri*[3]	Bousquet & Laplante (1999) as cited in Beutel et al. (2016)
Tachyoryctes spp.	*Epitoxus wittei*[1]	Jeannel & Paulian (1945), Yélamos (1997)
Neotoma spp.	*Hister humilis*[1/3?], *H. sarcinatus*[1/3?], *H. lucanus*[1/3?], *Onthophilus deflectus*[2], *O. intermixtus*[?], *Euspilotus rubriculus*[3?], *Gnathoncus interceptus*[?]	Beutel et al. (2016), Caterino (2002), Kovarik (1994), Pinto & Ribeiro (2011)
Prometheomys schaposchnikowi	*Margarinotus prometheus*[1], *Onthophilus convictor*[1]	Kryzhanovskij (1977), Reichardt (1941)
Cricetus cricetus *Cricetulus* spp.	*Gnathoncus disjunctus suturifer*[2], *Pholioxenus quedenfeldti*[2], *P. schatzmayri*[2], *Onthophilus punctatus*[2]	Kovarik (1994), Kryzhanovskij (1977), Reichardt (1941)
Meriones spp.	*Pholioxenus phoenix*[1/2?], *Erebidus vlasovi*[2], *Gnathoncus disjunctus suturifer*[2], *G. kiritshenkoi*[2], *G. pygmaeus*[1/2?], *Microsaprinus therondianus*[2]	Kryzhanovskij (1977), Reichardt (1941), Tishechkin & Lackner (2012)
Rhombomys opimus	*Erebidus vlasovi*[2], *E. reichardti*[1], *Gnathoncus kiritshenkoi*[2], *Pholioxenus orichalceus*[2], *Saprinillus paromaloides*[1/2?], *Dendrophilus sulcatus*[3]	Kryzhanovskij (1977), Lackner (2009) Reichardt (1941), Tishechkin & Lackner (2012)
Pachyuromys duprasi	*Paravolvulus refector*[1], *P. binaevulus*[1]	Kryzhanovskij (1977), Reichardt (1941)
Microtus spp. *Mus* spp.	*Margarinotus hailar*[2], *Onthophilus punctatus*[2], *Gnathoncus disjunctus suturifer*[2]	Kryzhanovskij (1977), Reichardt (1941)
Ochotona spp.	*Margarinotus hailar*[2], *Dendrophilus proditor*[2/3?]	Kryzhanovskij (1977), Reichardt (1941)
Oryctolagus cuniculus	*Onthophilus punctatus*[2], *Pholioxenus quedenfeldti*[2]	Kryzhanovskij (1977), Reichardt (1941)
Talpa europaea	*Margarinotus merdarius*[3], *Onthophilus punctatus*[2], *Saprinus rugifer*[2]	Kryzhanovskij (1977), Reichardt (1941)
Meles meles	*Pholioxenus quedenfeldti*[2], *Dendrophilus sulcatus*[3], *Onthophilus punctatus*[2]	Kovarik (1994), Kryzhanovskij (1977), Reichardt (1941)
Taxidea taxus	*Margarinotus pluto*[2]	Caterino (2010)
Vulpes vulpes	*Gnathoncus kiritschenkoi*[2], *Erebidus vlasovi*[2]	Olexa (1984)

Bird nests (especially cavity nests or burrow nests) host numerous Histeridae species. Some species of genus *Gnathoncus* (e.g., the Palearctic *G. nannetensis, G. buyssoni, G. rotundatus, G. communis, G. nidorum*) are often collected in nests of various birds (including passerines, owls, Falconiformes, storks etc.) (Lundyshev & Tishechkin 2013). *Euspilotus perrisi* occurs in the nests of the European bee-eater (*Merops apiaster*) and is rarely found elsewhere (Lackner 2010). *Saprinus rugifer* is most often collected in sand martin (*Riparia riparia*) nests, but is also known to be found in mole burrows (Kryzhanovskij & Reichardt 1976; Lackner 2010). Several species of genera *Eremosaprinus*, *Pholioxenus*, *Tomogenius* and *Saprinus* also occasionally occur in bird nests (Lackner 2010; Lackner & Leschen 2017). Reichardt (1941) mentiones an occasional association of *Dendrophilus punctatus* with nests in hollow trees. North American saprinines strongly associated with bird nests include *Geomysaprinus obscurus* (from nests of burrowing owl *Athene cunicularia hypogea*) (Lee & Ryckman 1953) and *Strigister tecolotito* (two owl species – *Megascops asio*, *Glaucilium brasilianum*) (Caterino et al. 2013). Other Nearctic taxa occasionally visit bird nests (Beutel et al. 2016). Several Saprininae species have been found in the burrows of the African penguin (*Spheniscus demersus*) together with a histerine species *Atribalus wolfaardti* which has only been collected from the penguin's nests or sand near them (Gomy & Perreau 2001). It is expectable that many other Histeridae species are more or less closely associated with various bird nests, but only limited amount of data is available from outside of the Palearctic and Nearctic regions.

Lizard burrows: The North American gopher tortoise (*Gopherus polyphemus*) is the only lizard whose burrows host obligatory nidicolous histerids. Two Saprininae species – *Chelyoxenus xerobatis* and *Geomysaprinus floridae* – inhabit its burrows (Bolt 2017; Young & Goff 1939). *Chelyoxenus xerobatis* feeds especially on *Eutrichota gopheri* – also a regular inhabitant of the tortoise's burros (Deyrup 2007). *Saprinus ferrugineus* is an occasional visitor of the tortoise's burrows (Young & Goff 1939). Olexa (1984) reported collecting some specimens of *Pholioxenus orichalceus* (mistakenly quoted as *P. schawalleri* by Beutel et al. (2016)) from the Horsfield's tortoise (*Testudo horsfieldii*) tunnels.

4.3.7 Psammophily

Some Saprininae lineages have adapted to life in sand. Many of them have evolved unique adaptations for digging in sand. These include reduced or missing protarsi, enlarged protibiae, setae on hypomera, pleura and on the outer margin of meso- and metatibiae (Beutel et al. 2016; Lackner et al. 2019).

Lackner et al (2019) divided saprinine species with sand association into three ecological units – xerophiles, semi-psammophiles and ultrapsammophiles.

Xerophiles live in dry areas and are sometimes collected on sandy soils, but can also be found elsewhere. They prey on larvae in carcasses or dung.

Semi-psammophiles bear some psammophily adaptations, which are not extreme (setose underside etc., Figure 19B). They are rarely found away from sandy substrate, but they do not dig deep in the sand. The category is represented by species of *Xerosaprinus*, *Styphrus* etc. The authors pointed out so-called psammolittoral taxa as a part of the semi-psammophilous group. These species are found in coastal sandy areas. Their coxa and femora are enlarged to accommodate the large muscles needed for digging in damp sand (Figure 19C). They feed on larvae under rotting algae, wrack etc. Some species of *Pachylopus*, *Hypocaccus*, *Hypocacculus* and other genera fall in this group (Beutel et al. 2016; Yélamos 1989). Species from other subfamilies can also be found in rotting material on sand dunes or beaches along the coast (e.g., *Tribalus scaphidiformis* (Tribalinae), *Halacritus* spp. (Abraeinae)) (Gomy 1976; Kovarik 1994; Yélamos 1989).

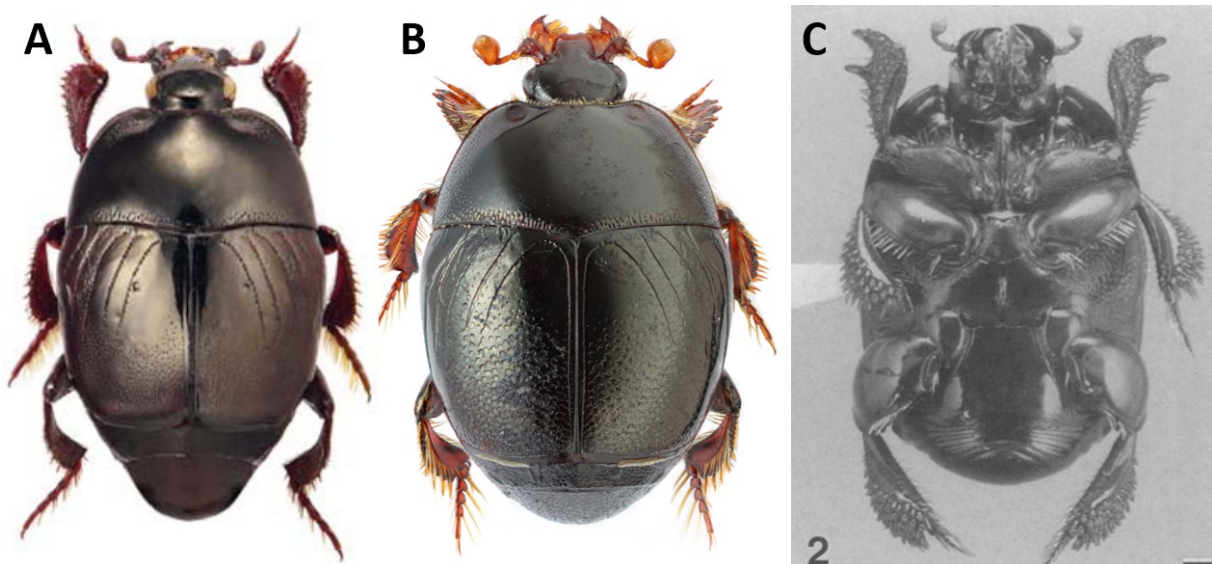Figure 19 Saprininae species with various sand associations; A – *Saprinus semistriatus*, non-psammophilous species (adopted from Lackner (2015)); B – *Styphrus corpulentus* – semi-psammophilous species, with setae as an adaptation for life in sand (photo by M. E. Smirnov); C – *Pachylopus rossi*, psammolittoral species, enlarged femora for large muscles used for digging in damp sand (adopted from Kovarik et al. (1999))

Ultra-psammophiles can only be found in sand dunes and are often buried very deep (Olexa (1990) reports *Ctenophilothis* and *Philothis* found down to 50 cm under the surface). These species bear the most extreme adaptations, such as reduced or missing protarsi (Figure 20B), shovel-like protibiae and long and thick setae, which allow them to literally swim in the sand (Olexa 1990). They prey on Diptera and Coleoptera (mostly Tenebrionidae and Scarabaeidae) larvae that feed on decomposing roots of the sparse vegetation on sandy dunes (Beutel et al. 2016; Olexa 1990). They are found in Nearctic, Palearctic and Afrotropical deserts – e.g., *Philoxenus* in Sonora desert, *Teramopoton* and *Paraphilothis* in Namib desert, *Ctenophilothis* (Figure 20A), *Philothis* and *Xenonychus* in Sahara desert and Kara Kum, Kizil Kum and other central Asian deserts (Mazur 2011; Olexa 1990).
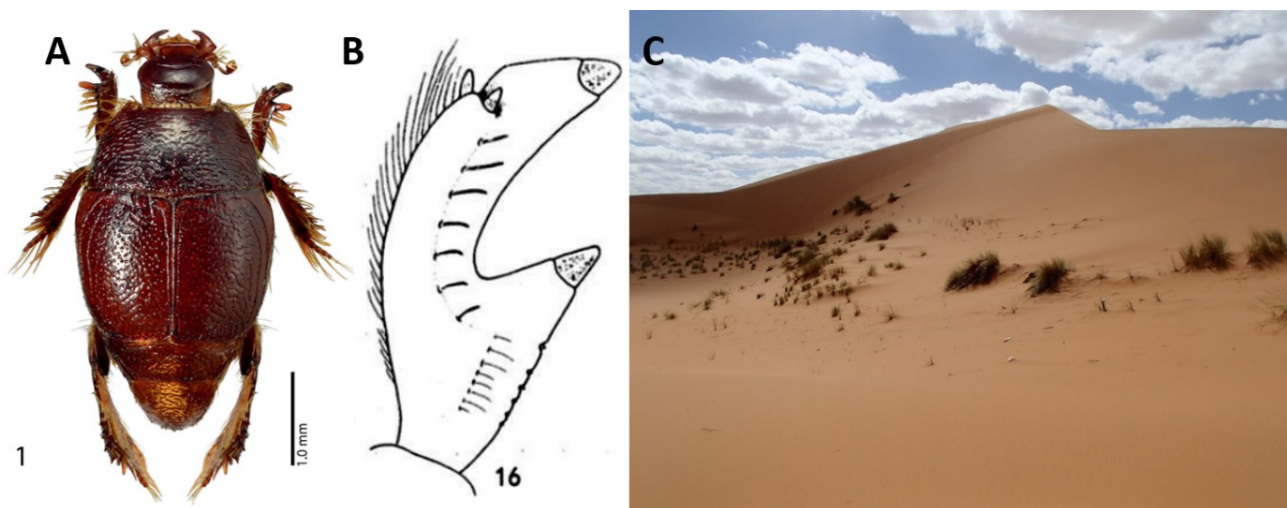

Figure 20 Ultra-psammophilic adaptations. A – *Ctenophilothis altus* (adopted from Lackner (2014b)), B – *Philothis pierrei* – protibia, protarsus completely reduced (adopted from Olexa (1990)), C – sand dunes of Erg Chebbi in Western Sahara (Morocco) – habitat of *Ctenophilothis chobauti*

Some species may be found on sandy or gravely river banks but they do not bear any modifications for life in sand (Lackner et al. 2019).

4.3.8 Cave dwelling

Relatively few Histeridae genera are found in caves. True troglobites (found exclusively or almost exclusively in caves) are minute histerids of the subfamilies Abraeinae (*Spelaeacritus*, *Spelaeabraeus, Iberacritus vivesi*) and Dendrophilinae (*Sardulus*, *Troglobacanius*, *Anapleus wenzeli*) (Beutel et al. 2016; Vomero 1982).

Insect troglobionts often bear specific adaptations for life in caves – elongate body appendages, reduced or lost eyes, depigmentation, loss of flight ability, reduced or lost wings, fused elytra and others (Culver & Pipan 2018). *Spelaeacritus anophthalmus* (Figure 21) accumulates these adaptations to the highest extent among Histeridae – namely elongate body appendages, complete loss of eyes and fused elytra (Jeannel 1934). Its head is (unlike in other histerids) quasi-prognathous (Beutel et al. 2016) and the beetle has completely lost the ability of retracting it under pronotum (a typical defense mechanism in other histerids), as predation threads from the ground surface were no longer present (Jeannel 1934). Jeannel (1934) described it from a single specimen found in a cave in Turkey. Mazur (1977) later reported several other specimens that were collected by sifting, so the species is probably also endogean. *Spelaeabraeus* contains several troglobiotic species distributed in central Italy (Mazur 2011). Some of them (e.g., *S. agazzi*) have also been reported as endogean (Vomero 1982). Blind *Iberacritus vivesi* has only been collected among decomposing wood and plant debris in the small cave Cova d'En Janet in Catalonia, Spain (Yélamos 1994). *Sardulus* contains several strictly

cavernicolous species known from caves in Sardinia, Italy (Casale et al. 2006; Magrini & Fancello 2005). Species of strictly troglobiotic *Troglobacanius* have been described from several caves in various parts of Mexico, usually found in association with bat colonies, which included vampire bats (Vomero 1973a). *Anaplaeus wenzeli* was collected in a cave in Chiapas, Mexico. It appeared in large numbers on fungal colonies covering rotting wood in the cave, where it presumably consumed small arthropods based on examination of its gut content (Vomero 1977).
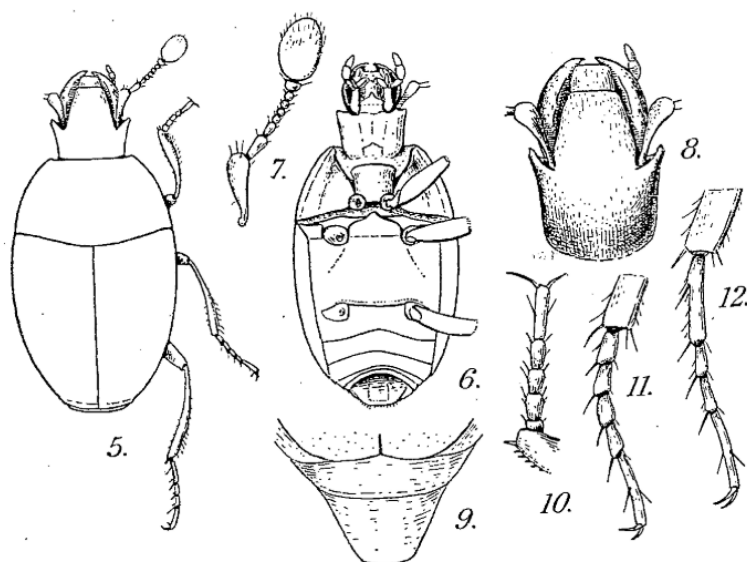

Figure 21 *Spelaeacritus anophthalmus*. Adopted from Jeannel (1934)

Several other Histeridae species not associated with caves have reduced eyes and flight ability. *Anophthaeletes rousi* is a blind Palearctic species from Georgia that has been collected inside a rotting *Quercus* trunk (Olexa 1976). *Iberacritus ortunoi* inhabits debris rich soil in Catalonia, Spain, where it has been found down to 20 cm under surface near tree roots (Yélamos 1994). *Aeletes gemmula* is an endogean species distributed on the island of Gomera and can be found in rotting wood under surface (Vit & Masoliver 2004; Yélamos 1994). North American *Geocolus caecus* lives in soil or litter and is blind and micropterous (Beutel et al. 2016; Vomero 1973b).

Many species have been collected in caves, but they do not bear any morphological adaptations for troglobiotic life. They are usually attracted to bat guano (and prey on Diptera larvae that develop there) and some can be found outside of caves as well. Taxa reported from caves include: Saprininae: *Gnathoncus breviscernus*, *G. cerberus*, *G. cavicola*, *Afroprinus cavicola*, *Tomogenius incisus*, *T. ripiciola*, *T. motocola*, *T. papuanensis*, *Euspilotus rubriculus*, *E. scrupularis*, *E. burgeoisi*, *E. turikensis*, *E. modestus*, *E. sterquilinus*, *Acritus analis;* Tribalinae: *Epierus antillarum*, *E. pulicarius*; Dendrophilinae: *Dendrophilus sulcatus, Carcinops troglodytes, Bacanius* rugisternus; Histerinae*: Phelister globiformis, Operclipygus tripartitus, O. teapensis, O. schlingeri* (Beutel et al. 2016; Lackner 2013, 2020). Lackner (2013) hypothesised that the mentioned Saprininae species might represent an early stage of cave colonisation.

5 Summary and discussion about life-history strategies evolution

Based on the above-presented information about the ecology and evolution of the Histeroidea, I here try to comment on the evolution of their life strategies. Unfortunately, the phylogenetic data are relatively limited. Infra-subfamily level is yet to be addressed in most Histeridae subgroups. It is thus difficult to make conclusions about life-history shifts that may have happened on the species, generic and tribal levels. Therefore, I only adress the aspects of histeroid evolution in which, based on current knowledge, some sort of discussion is possible.

5.1 Evolution of feeding habits

The predaceous feeding habit of larvae and adults is plesiomorphic. Both Sphaeritidae and Synteliidae are predators (sphaeritids may also consume tree sap etc., but it is most likely not the main food source). All Histeridae larvae are also predaceous and so are the adults in most species. Adults of several taxa (most genera of Tribalinae, *Epiechinus* and most species of Bacaniini) have been reported to be primarily sporophagous (for more information see chapter 4.2). They even have specialised maxillary setae that work as spore-gathering combs.

The sporophagy, associated with mouthpart adaptations, evolved multiple times. Kovarik (1994) distinguished two major types of modified maxillary galea serving for spore gathering in Tribalinae, suggesting that their fungivory originated at least twice independently. This is consistent with the results of Zhou et al. (2020), who proposed the polyphyly of Tribalinae. A robust phylogenetic analysis, with important tribaline genera included, is needed for more precise considerations of the matter.

The onthophiline genus *Epiechinus* has an even different type of maxillary galea (Kovarik 1994). According to Zhou et al. (2020), a part of Onthophilinae (*Onthophilus* and *Epiechinus*) forms a lineage nested within Dendrophilinae and standing as sister to Bacaniini (also mostly sporophagous). It is possible that spore feeding is a synapomorphy of these two sister lineages. Multiple species of *Onthophilus* have swapped to filtration (see chapter 4.2) performed with setae on mandibles and on maxillary galea (Kovarik 1994). Potentially, the spore-gathering setose combs could have served as a preadaptation for filter-feeding. Several species of *Onthophilus* remained at least partially sporophagous while some are also facultative predators (Beutel et al. 2016; Kovarik 1994).

5.2 Evolution of inquilinism

Various forms of inquilinism have arisen many times within Histeridae.

Two highly derived myrmecophilous lineages (Haeteriinae and Chlamydopsinae) evolved independently. They are greatly adapted for ant inquilism in their morphology, behaviour, chemical signals etc. Both lineages are mostly host specific and may be subject to a strong coevolution with the ants (Caterino & Dégallier 2007; Tishechkin 2007). Host switching (even between ant subfamilies or ants and termites) must have occurred repeatedly in the evolution of both groups. The myrmecophily of Haeterinae is at least 99 million years old according to the fossil record (see chapter 3.1). It is probably the capability to switch hosts that has allowed great longevity of their symbiosis with ants (Zhou et al. 2019). Abandoning a specialised strategy such as integrated myrmecophily seems improbable (Tishechkin 2007). However, it probably happened at least once in Haeteriinae. *Scapicoelis tibialis* has been reared from a spider egg sac (Kapler 1999) and an adult has been observed on vegetation (Degallier 1979). According to Caterino & Tishechkin (2015), the sister lineage

of Haeteriinae is formed by *Paratropus* and *Coelocraera*. Both genera are associated with ants or termites in some way.

According to Lackner (2014), myrmecophily in Saprininae has probably evolved three times independently – in *Myrmetes*, in *Phoxonotus* and in a clade containing *Saprinodes, Euspilotus (Platysaprinus)* and *Iridoprinus*. Interestingly, in the case of *Phoxonotus,* tree topology indicates a possible transition from mammal inquilinism to myrmecophily. The author later published an updated phylogeny (Lackner et al. 2019) which has placed *Myrmetes* in close relation with *Gnathoncus* mammal inquilines, suggesting the shift from mammal to ant inquilinism occurred multiple times. Vertebrate inquilinism is very common in Saprininae. It is also the only histerid subfamily, which has big, strictly nidicolous, lineages. In fact, Lackner (2014) hypothesised that inquilinism might be an ancestral state in Saprininae.

We can find numerous (both ant and vertebrate) inquilines among Histerinae. This group appears to have a tendency towards inquilinism as it has arisen multiple times across various genera, often only isolated species possessing such a lifestyle (Caterino & Tishechkin 2015). Zhou et al. (2020) proposed that the great diversity of Histeromorphae is caused by inquilinistic relationships that are so common within this group.

Multiple Onthophilinae species of the genus *Onthophilus* are also vertebrate symbionts and at least one species is myrmecophilous.

Inquilinism in other lineages is scarce and it is usually found only in individual species. Furthermore, associations in these cases are usually rather weak and non-obligatory.

Vertebrate inquilinism is probably a relatively flexible strategy and lineages can easily adopt it or abandon it. Shifts from vertebrate inquilinism to myrmecophily occurred multiple times in Saprininae, Histerinae and possibly also in Onthophilinae. Both mammal and social insect inquilinism have played an important role in the evolution of the crown groups of Histeridae.

5.3   Evolution of flat and cylindrical body shape in subcortical species

Cylindrical body shape has evolved in several lineages independently. Firstly, all species of Synteliidae are cylindrical and, with the exception of *Syntelia westwoodi,* they are all subcortical. Jiang & Wang (2021) described a cylindrically shaped *Syntelia* from Late Cretaceous. Secondly, the genus *Platysoma* has multiple cylindrically shaped species. Unfortunately, the phylogenetic data are missing for the genus and we cannot determine whether cylindricity in *Platysoma* has multiple origins or not. Lastly, a strongly elongated cylindrical body shape can be found within all Niponiinae, Trypeticini and Trypanaeini and in many taxa of Teretriini. According to Zhou et al. (2020), these taxa form a monophyletic clade within Abraeinae. This suggests that the cylindrical body shape in these lineages might be of the same origin. Therefore, we can conclude cylindricity evolved at least thrice independently.

Dorsoventral flattening occurred multiple times in Histerinae. According to a recent phylogenetic study on Exosternini and related taxa (Caterino & Tishechkin 2015), flat body shape appeared at least five times in Histerinae. The internal phylogeny of the Dendrophilinae is rather incompletely known, but it appears that the tribe Paromalini, which contains all flat-bodied representatives of Dendrophilinae, is monophyletic (Zhou et al. 2020). Caterino (2021) described a slightly dorsoventrally flattened dendrophiline *Druantia aeterna* from a fossil dating to 99 mya. I possess a dorsoventrally flat specimen from Burmese amber likely belonging in Platysomatini.

5.4 Evolution of psammophily in Saprininae

According to Lackner et al. (2019), psammophily in Saprininae first appeared in the Paleocene. According to the authors, rapid radiation of sand-associated taxa occurred during the Paleocene-Eocene thermal maximum (PETM) and continued through the Early Eocene Climatic Optimum. Although humidity increased in many places during the PETM, there were probably several aridification centres, incl. North Africa where many psammophilic species occur today (Carmichael et al. 2017).

"Ultrapsammophily" evolved at least three times in different regions – in the Nearctics (*Philoxenus*), in the Afrotropics (*Terametopon*) and in the Palearctic region (*Ctenophilothis, Philothis, Xenonychus*). The ultrapsammophilous *Philoxenus* is nested among psammolittoral taxa. Sister lineage of the Palearctic ultrapsammophilous clade is represented mostly by species found on sandy coast environemnets. This suggests a possible mechanism of origin for ultrapsammophily in ancestors that inhabited the sandy substrates along the coast. If the coast bordered a sandy desert, the coastal lineage probably gradually invaded the sand dunes and evolved adaptations for ultrapsammophily.

5.5 Final words

Histeroid beetles truly represent an interesting group. Although entomologists have studied them for more than 250 years, many aspects of their life and evolution remain obscure and further research will surely bring interesting discoveries. It is my hope that I will also be able to contribute to the understanding of this fascinating group through my own future work.

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7 Attachments

7.1 Nomenclature

The species and genus names of the histeroid taxa cited in this thesis follow Mazur (2011). The authorship of the taxa not included in Mazur's catalogue (fossils, Synteliidae, Sphaeritidae or described after 2011) and cited in the text is as follows:

Synteliidae:

Syntelia sunwukong Jiang & Wang, 2021

Syntelia westwoodi Sallé, 1873

Sphaeritidae

Sphaerites glabratus (Fabricius, 1792)

Cretohisteridae:

Cretohister sinensis Zhou, Caterino, Ślipiński & Cai, 2018

Histeridae:

Afroprinus cavicola Lackner, 2013

Amplectister tenax Caterino and Maddison, 2018

Antigracilus costatus Zhou, Caterino, Ren & Ślipiński, 2020

Bacanius goorskii Alekseev & Bukejs, 2021

Bacanius kirejtshuki Sokolov & Perkovsky, 2020

Carcinops donelaitisi Alekseev, 2016

Carinumerus maddisoni Caterino, 2021

Carinumerus yingae (Jiang, Shi & Wang, 2020)

Cretonthophilus tuberculatus Caterino, Wolf-Schwenninger & Bechly, 2015

Druantia aeterna Caterino, 2021

Hister aemulus Heer, 1862

Hister antiquus Heer, 1862

Hister cerestensis Degallier, Garrouste & Nel, 2019

Hister coprolithorum Heer, 1862

Hister maculigerus Heer, 1862

Hister marmoratus Heer, 1862

Hister mastodontis Heer, 1862

Hister morosus Heer, 1862

Hister vetustus Heer, 1862

Hypocaccus hungaricus Lackner & Seres, 2018

Iridoprinus myrmecophilus Lackner & Leschen, 2017

Onthophilus intermedius Handschin, 1944

Pantostictus burmanicus Poinar & Brown, 2009

Phasmister cristatus Caterino, 2021

Phelister warneri Caterino & Tishechkin, 2019

Plegaderus pitoni (Theobald, 1935)

Promyrmister kistneri Zhou, Ślipiński & Parker, 2019

Saprinus rarus Lackner & Leschen, 2017

Strigister tecolotito Caterino, Tishechkin & Proundfoot, 2013

Trypanaeus hispaniolus Chatzimanolis, Caterino & Engel, 2006

Xestipyge ikanti Alekseev, 2016

Yethiha peregrina Caterino, 2021