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Review

The Fossil Record of Darkling Beetles (Insecta: Coleoptera: Tenebrionidae)

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Abstract: The fossil record of Tenebrionidae (excluding the Quartenary) is presented. In total, 122 fossil species, clearly belonging to the family, are known; some beetles were determined only to genus; 78 genera are listed in the fossil record, including 29 extinct genera. The great diversity of tenebrionids occurs in the Lower Cretaceous Lagerstätte of China (Yixian Formation), Middle Paleocene of France (Menat), Lower Eocene deposits of Germany (Geiseltal), Upper Eocene Baltic amber (Eastern Europe), Upper Eocene deposits of Florissant Formation (USA) and Miocene (Dominican amber). Tenebrionids of the following major lineages, including seven subfamilies, are currently known in the fossil record. These include the lagrioid branch (Lagriinae, Nilioninae), pimelioid branch (Pimeliinae), and tenebrioid branch (Alleculinae, Tenebrioninae, Diaperinae, Stenochiinae). The importance of the fossil record for evolutionary reconstructions and phylogenetic patterns is discussed. The oldest Jurassic and Early Cretaceous darkling beetles of the tenebrionoid branch consist of humid-adapted groups from the extant tribes Alleculini, Ctenopodiini (Alleculinae), and Alphitobiini (Tenebrioninae). Thus, paleontological evidence suggests that differentiation of the family started at least by the Middle Jurassic but does not indicate that xerophilic darkling beetles differentiated much earlier than mesophilic groups.

Keywords: fossils; Tenebrionidae lineages; fossil history; catalogue; evolutionary reconstructions

1. Introduction

Tenebrionidae is one of the largest beetle families, comprising nearly 20,000 extant species and 2300 genera in the World [1]. The monophyly of the family was justified by many authors in the 20th and 21st centuries [1] and was also recently supported after the analysis of eight gene markers, but at least two large subfamilies, Tenebrioniae and Diaperinae, seem to be paraphyletic or polyphyletic [2]. The systematics of tenebrionid beetles was modified by many authors. The currently accepted classification of the family is based on the analysis of multiple external and internal morphological structures [1,3–10] and includes 11 subfamilies [10–13] from lagrioid, pimelioid, and tenebrionoid branches [11]. Fossil Tenebrionidae have been used in evolutionary reconstructions [14,15]. The fossil record of darkling beetles is highly fragmented. Matthews et al. [1] briefly discussed the fossil record of Tenebrionidae, but since that time, important new data have been published. In the present work, the current data on extinct Tenebrionidae are summarized and analyzed. This includes a new catalogue of extinct darkling beetles, critical evaluation of fossil taxa, questions of systematics, and discussions of evolutionary scenarios and paleo-reconstructions.

2. Material and Methods

Material from European and Asian museums as well as from private collections were used by the author in previous original descriptions of fossil taxa (see Table 2 and References for taxa, described by M.V. Nabozhenko and co-authors) with depositories listed in the original descriptions. In addition, a detailed analysis of the cited literature was included.

The following internet resources were used for catalogue numbers and the age of the fossils:

- Fossilworks: http://fossilworks.org/,
- International Commission on Stratigraphy: http://www.stratigraphy.org/,
- Catalogue of fossil Tenebrionidae: https://www.zin.ru/Animalia/Coleoptera/rus/teneb_ff.htm.

Authors and years of extant taxa were added according to recommendations of the International Code of Zoological Nomenclature in the redaction of 1999 (https://www.iczn.org/) and are not considered as cited literature to avoid excessive citation. References for all these taxa including authors and years of tribes and subfamilies can be found in many current catalogues.

3. Brief History of the Study of Fossil Tenebrionidae

Studies of fossil tenebrionids began with the papers by E.F. Germar [16] of the description of *Tenebrio effossus* from the Rott Formation (Upper Oligocene/Lower Miocene) of Germany. Brothers C. and L. Heyden described extinct Tenebrionidae from the same formation [17,18], and O. Heer added many publications of fossil tenebrionids from the Miocene of Germany [19,20], Middle Cretaceous of Sakhalin, Russia [21] and Paleocene of Greenland [22]. The first fossil darkling beetles from North America (mostly Alleculinae) were described by S.H. Scudder [23,24] and Wickham [25–28] from the Eocene. R. Klebs [29] summarized data on beetles from Eocene Baltic amber with a list of genera and species (including Tenebrionidae). Later, materials of R. Klebs were lost, and the taxa mentioned in this work are impossible to verify.

The publications on fossil Tenebrionidae of the 19th century and beginning of the last century are characterized by rather short descriptions and unclear illustrations; thus, these described taxa need to be revised.

In the middle of the 20th century, the greatest contribution to the study of fossil tenebrionids was made by H. Haupt [30] who described many genera and species from the Eocene of Germany (Geiseltal). Haupt used homologization of elytral venation for the identification of his taxa, most of which need further revision. L. Medvedev [31] qualitatively described and illustrated a comb-clawed beetle from the Mid/Late Jurassic of Karatau (Kazakhstan). Later, studies of fossil Tenebrionidae were resumed only at the end of the 20th century. S.G. Larson [32], and F. Hieke and E. Pietrzeniuk [33] greatly contributed to the knowledge on tenebrionids from Eocene Baltic amber. U. Spahr [34] published a detailed catalogue of all beetles from fossil amber and copal. Chinese authors [35,36] described several Alleculinae from the Miocene of China (Shanwang). Tenebrionidae from the Miocene Dominican amber were studied by Z. Kaszab and W. Schawaller [37] and later were summarized by Doyen and Poinar [38] who described many extinct darkling beetles from the subfamilies Lagriinae, Pimeliinae, Tenebrioninae, Diaperinae, and Stenochiinae.

The greatest progress in the study of extinct Tenebrionidae has been achieved in the last 10 years. A.G. Kirejtshuk et al. [39] published the very important work with a catalogue of fossil Tenebrionidae (more than 100 extinct taxa). This catalogue is regularly modified at the website "Beetles and coleopterologists" [40]. Our knowledge about Mesozoic darkling beetles has been expanded [41–43] with the publications of fossils Alleculinae and Tenebrioninae from the Yixian Formation of China. A significant contribution was made to the knowledge of Tenebrionidae from the Middle Paleocene deposits of Menat, France [44,45], European Eocene ambers (Baltic and Oise) [46–55], and the Oligocene/Miocene Dominican amber [56,57]. The taxonomic position of some genera, which were originally included to Tenebrionidae, was revised and corrected by Kirejtshuk et al. [58].

4. Catalogue of Fossil Tenebrionidae

Different catalogues were published for Mesozoic Tenebrionidae [59], darkling beetles from ambers [34], from Dominican amber [60], etc., but a complete catalogue of Tenebrionidae was compiled by Kirejtshuk et al. [39] and regularly updated on the website "Beetles (Coleoptera) and coleopterists" by Kirejtshuk and A.G. Ponomarenko [40].

A. Handlirsch [61] listed many doubtful taxa (such as *Pseudotenebrio* Weyenbergh, 1869, etc.), which can belong to any beetle family. These taxa are not included in the catalogue below.

The open catalogue of Kirejtshuk and Ponomarenko [40] requires updating with taxonomic changes. As a result, the present study is the most up to date catalogue of extinct Tenebrionidae. At present, 122 species of fossil Tenebrionidae in the time span of 201–11.6 Ma are known (Tables 1 and 2), some of which have been identified only to genus.

Table 1. Abbreviations of fossil deposits, used in the paper (made using data from the website Fossilworks: http://fossilworks.org/ and Catalogue of fossil Tenebrionidae: [39,40]; https://www.zin.ru/Animalia/Coleoptera/rus/teneb_ff.htm).

Fossil Deposits	Era(period) Age, Ma
Early Jurassic, Rhaetian/Hettangian; Switzerland: Aargau, Schambelen	Mz(Ju) 201.6–196.5
Middle/Late Jurassic, Callovian/Oxfordian; Kazakhstan: Karatau	Mz(Ju) 164.7–155.7
Early Cretaceous, Aptian; China: Huangbanjigou, Chaomidian	Mz(Cr) 125.5–122.5
Early Cretaceous, Santonian; Russia: Sakhalin, Mgachi	Mz(Cr) 85.8–84.9
Early Paleocene, Danian; Argentina: El Sunchal	Pg(Pc) 66–55.8
Middle Paleocene, Selandian; Denmark, Greenland: Aumarutigsat, Haseninsel (Hareøen),	Pg(Pc) 61.7–58.7
Middle/Late Paleocene, Selandian/Thanetian; France: Menat	Pg(Pc) 61–56
Earliest Eocene, Oise amber, Ypresian; France: Le Quesnoy	Pg(Eo) 55.8–48.6
Early Eocene, Ypresian; Canada: Whipsaw Creek	Pg(Eo) 55.8–40.4
Middle Eocene, Lutetian; Germany: Messel Pit	Pg(Eo-Mess) 48.6–40.4
Middle Eocene, Lutetian; Germany: Geiseltal Halle	Pg(Eo-Geis) 48.6–40.4
Middle Eocene, Lutetian; United Kingdom: Bournemouth	Pg(Eo-Bour) 48.6–40.4
Late Eocene, Baltic Amber, Priabonian; coasts of the Baltic Sea	Pg(Eo-BA) 37.2–33.9
Latest Eocene, Priabonian; USA, Colorado: Florissant, Twin Creek, Front Range near Pike's Peak	Pg(Eo-Flor) 37.2–33.9
Early Oligocene, Rupelian; France: Alsace, Haut-Rhine, 5 km SW Mulhouse, Brunstatt	Pg(Og) 33.9–28.4
Late Oligocene/early Miocene, Chattian/Aquitanian; Germany: Rott	Ng(Mi) 28.4–23
Early Miocene, Aquitanian; Switzerland: Lausanne, Molasse	Ng(Mi) 23–20.4
Early Miocene, Mexican amber, Aquitanian/Burdigalian; Mexico: Simojovel area, Chiapas	Ng(Mi) 23–16
Early Miocene, Burdigalian; China: Linqu County, Shanwang	Ng(Mi-Shan) 20.4–16
Early Miocene, Burdigalian; Greece: Kumi, Euboea	Ng(Mi-Kumi) 20.4–16
Early Miocene, Dominican amber, Burdigalian; Dominican Republic	Ng(Mi-Dom) 20.4–13.7
Middle Miocene, Langhian/Serravallian; Germany: Lower Saxony, Salzhausen	Ng(Mi) 16.0–11.6
Middle Miocene, Serravallian; Germany: Baden-Württemberg, Oeningen	Ng(Mi)12.7–11.6

Table 2. Catalogue of extinct darkling beetles (excluding Quartenary), based on the checklist of fossil Tenebrionidae by Kirejtshuk et al. [39], with additions and corrections; †—extinct genera.

No.	Taxon	Age and Site of Finding	Sources
Subfamily Lagriinae			
Tribe Lagriini Latreille, 1825			
1	*Lagria* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
2	*Statira* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
3	*Statira baltica* Telnov, Bukejs et Merkl, 2019	Pg(Eo-BA) 37.2–33.9	[55]
4	*Statira dermoidea* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Tribe Laenini			
5	*Laena* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,62,63]
Tribe Gonialaenini Nabozhenko, Telnov et Bukejs, 2019			
6	*Gonialaena*† *groehni* Nabozhenko, Telnov et Bukejs, 2019	Pg(Eo-BA) 37.2–33.9	[51]
Tribe Lupropini Lesne, 1926			
7	*Luprops* sp.	Pg(Eo-BA) 37.2–33.9	[29]
8	*Lorelus angulatus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
9	*Lorelus foraminosus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
10	*Lorelus minutulus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
11	*Lorelus wolcotti* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Tribe Belopini Reitter, 1917			
12	*Yantaroxenos*† *colydioides* Nabozhenko, Kirejtshuk et Merkl, 2016	Pg(Eo-BA) 37.2–33.9	[50]
Subfamily Pimeliinae			
Tribe Asidini Fleming, 1821			
13	*Asida* (*Planasida*) *groehni* F. Soldati et Nabozhenko (2017	Pg(Eo-BA) 37.2–33.9	[53]
14	*Pelecyphorus* (*Stenosides*) *primus* (Wickham, 1910) (*Ologlyptus*), transferred to *Pelecyphorus* by F. Soldati & Nabozhenko (2017)	Pg(Eo-Flor) 37.2–33.9	[26,39,53]
Tribe Stenosini Schaum, 1859			
15	*Miostenosis*† *lacordairei* Wickham, 1913	Pg(Eo-Flor) 37.2–33.9	[27,39]
Tribe Edrotini Lacordaire, 1859			
16	*Trientoma hascens* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Subfamily Alleculinae			
Tribe Alleculini Laporte, 1840			
Subtribe Alleculina Laporte, 1840			
17	*Jurallecula*† *grossa* L. Medvedev, 1969	Mz(Ju) 164.7–155.7	[31,39,59,64]
18	*Allecula austriaca* Zhang, 1989	Ng(Mi-Shan) 20.4–16	[36,39]
19	*Allecula dominula* (Heer, 1847) (*Cistela*)	Ng(Mi) 12.7–11.6	[19,39,65]
20	*Allecula* sp.	Pg(Eo-BA) 37.2–33.9	[29,32]
21	*Hymenorus haydeni* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39]
22	*Hymenorus chiapasensis* Campbell, 1963	Ng(Mi) 23–16	[39,66]
23	*Hymenorus oculatus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
24	*Hymenalia* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
25	*Pseudocistela gracilis* Förster, 1891	Pg(Og) 33.9–28.4	[27,39,65]
26	*Parahymenorus* sp.	Ng(Mi-Dom) 20.4–13.7	[38,39]
27	*Lobopoda annosa* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
28	*Lobopoda* sp.	Ng(Mi-Dom) 20.4–13.7	[38,39]

Table 2. *Cont.*

No.	Taxon	Age and Site of Finding	Sources
Subtribe Mycetocharina Gistel, 1848			
29	*Mycetochara* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
30	*Mycetocharoides*† *baumeisteri* Schaufuss, 1888	Pg(Eo-BA) 37.2–33.9	[39,65,67,68]
Subtribe Gonoderina Seidlitz, 1896			
31	*Gonodera antiqua* (Wickham, 1913) (*Cistela*)	Pg(Eo-Flor) 37.2–33.9	[27,39]
32	*Gonodera vulcanica* (Wickham, 1914) (*Cistela*)	Pg(Eo-Flor) 37.2–33.9	[27,39]
33	*Gonodera baygushevae* Nabozhenko et I. Chigray, 2018	Pg(Eo-BA) 37.2–33.9	[54]
34	*Gonodera* sp. (*Cistela*); transferred to *Gonodera* by Spahr (1981)	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,69]
35	*Isomira* (*Mucheimira*) *avula* Seidlitz, 1896 (originally in the subgenus *Asiomira*; transferred by Nabozhenko et al. 2019)	Pg(Eo-BA) 37.2–33.9	[39,52,65]
36	*Isomira* (*Isomira*) *hoffeinsorum* Nabozhenko in Nabozhenko, I. Chigray et Bukejs, 2019	Pg(Eo-BA) 37.2–33.9	[52]
37	*Isomira* sp. aff. *hoffeinsorum*	Pg(Eo-BA) 37.2–33.9	[52]
38	*Isomira* (subgenus incertus) *florissantensis* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39]
39	*Isomira* (subgenus incertus) sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
40	*Capnochroa senilis* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39]
Tribe Cteniopodini Solier, 1835			
41	*Platycteniopus*† *diversoculatus* Chang, Nabozhenko, Pu, Xu, Jia et Li, 2016	Mz(Cr) 125.5–122.5	[43,59,64]
42	*Calcarocistela*† *kirejtshuki* Nabozhenko in Nabozhenko, Chang, Xu, Pu et Jia, 2015	Mz(Cr) 125.5–122.5	[42,59]
43	*Cteniopus* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,39]
44	*Cteniopinus* sp.	Pg(Eo-BA) 37.2–33.9	[33,39]
45	*Sinocistela*† *gymnelytra* Zhang, 1989	Ng(Mi-Shan) 20.4–16	[36,39]
46	*Sinocistela*† *silpha* Zhang, 1989	Ng(Mi-Shan) 20.4–16	[36,39]
Subfamily Tenebrioninae			
Tribe Palorini			
47	*Palorus* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,47,48,62,63]
48	*Palorus platycotyloides* Alekseev et Nabozhenko, 2017	Pg(Eo-BA) 37.2–33.9	[48]
49	*Vabole*† *triplehorni* Alekseev et Nabozhenko, 2015	Pg(Eo-BA) 37.2–33.9	[47,48]
Tribe Toxicini			
Subtribe Eudysantina			
50	*Wattius reflexus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Tribe Bolitophagini			
51	"*Bolitophagus*" *vetustus* Heyden et Heyden, 1866	Ng(Mi) 28.4–23	[18,39,70,71]
52	*Bolitophagus* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,61,69–75]
53	*Rhipidandrus quadripapillatus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
54	*Proteleates*† *centralis* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39] (as *Protelerates* in the tribe Blaptini)]

Table 2. *Cont.*

No.	Taxon	Age and Site of Finding	Sources
	Tribe Tenebrionini		
55	*Tenebrio primigenius* Scudder, 1879	Pg(Eo) 55.8–40.4	[23,70,71,76]
56	*Tenebrio effossus* Germar, 1837	Ng(Mi) 28.4–23	[16,39,70–72]
57	*Tenebrio senex* Heyden, 1859	Ng(Mi) 28.4–23	[17,39,70,71]
	Tribe Alphitobiini		
58	*Alphitopsis*† *initialis* Kirejtshuk, Nabozhenko et Nel, 2011		[41,59,64]
	Tribe Amarygmini		
59	*Meracantha lacustris* Wickham, 1909	Pg(Eo-Flor) 37.2–33.9	[28,39]
60	*Cymatothes dominicus* Doyen et Poinar, 1994	Pg(Eo-Flor) 37.2–33.9	[38,39,57]
	Tribe Helopini		
61	*Cryptohelops*† *menaticus* Nabozhenko et Kirejtshuk, 2014	Pg(Pc) 61–56	[44,49,52]
62	*Stenohelops* (*Stenolassus*) *klebsi* (Nabozhenko, Perkovsky et Chernei, 2016) (originally as *Nalassus*, was transferred to *Stenohelops* by Nabozhenko et al. (2019))	Pg(Eo-BA) 37.2–33.9	[49,52]
63	*Helops meissneri* Heer, 1847	(Ng(Mi) 12.7–11.6	[19,39,72,73]
64	“*Helops*” sp. (genus incerta sedis)	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,49,62,63]
	Tribe Triboliini		
65	*Tribolium* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,62,63]
66	*Hypodena marginalis* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
	Tribe Ulomini		
67	*Uloma sp.*	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,62,63]
68	*Uloma avia* C. Heyden, 1862	Ng(Mi) 28.4–23	[70,71,77]
	Tribe Pedinini		
	Subtribe Leichenina		
69	*Leichenum* sp.	Pg(Eo-BA) 37.2–33.9	[29,32,34,39,62,63]
	Tribe Opatrini		
	Subtribe Opatrina		
70	*Ephalus adumbratus* Scudder, 1900	Pg(Eo-Flor) 37.2–33.9	[24,39,45]
71	*Paleosclerum*† *pohli* Nabozhenko et Kirejtshuk, 2017	Pg(Pc) 61–56	[45]
72	*Ulus minutus* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39,45]
73	*Gonocephalum pristinum* (Heyden et Heyden, 1866)	Ng(Mi) 28.4–23	[18,39], [70] (as *Opatrum*), [71] (as *Opatrum*)
	Subtribe Neopachypterina		
74	*Eupachypterus*† *eocenicus*	Pg(Eo) 55.8–48.6	[45,46]
	Subfamily Diaperinae		
	Tribe Diaperini		
75	*Ceropria* (?) *messelense* Hornschemeyer, 1994	Pg(Eo-Mess) 48.6–40.4	[39,78]
76	*Platydema bethunei* Wickham, 1913	Pg(Eo-Flor) 37.2–33.9	[27,39]
77	*Platydema antiquorum* Wickham, 1913	Pg(Eo-Flor) 37.2–33.9	[27,39]
78	*Platydema geinitzi* Heyden et Heyden, 1866	Ng(Mi) 28.4–23	[18,39,70,71]

Table 2. *Cont.*

No.	Taxon	Age and Site of Finding	Sources
79	*Pentaphyllus cioides* Kirejtshuk, Merkl et Kernegger, 2008	Pg(Eo-BA) 37.2–33.9	[39]
80	*Liodema phalacroides* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
81	*Neomida senicula* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Tribe Scaphidemini			
82	New fossil genus† and a new species	Pg(Pc) 61–56	(Nabozhenko, Kirejtshuk, in litt)
Tribe Hypophlaeini			
83	*Corticeus tertarius* Vitali, 2007	Ng(Mi-Dom) 20.4–13.7	[56]
84	"*Hypophloeus*" sp. (*Corticeus*)	Pg(Eo-BA) 37.2–33.9	[34,79]
Tribe Gnathidiini			
Subtribe Anopidiina			
85	*Tyrtaeus azureus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
86	*Tyrtaeus elongatus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
87	*Tyrtaeus flavoantennatus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
88	*Tyrtaeus thoracicus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
89	*Tyrtaeus cupreorutilans* Vitali, 2008	Ng(Mi-Dom) 20.4–13.7	[57]
Subfamily Stenochiinae			
90	*Pseudohelops*† *groenlandicus* Haupt, 1950 (nom nov. by Haupt (1950) = *Helops molassicus* Heer, 1883 nec *Helops molassicus* Heyden, 1865)	Pg(Pc) 61.7–58.7	[22,30,39,70,71]
91	*Pyrochalcaspis*† *geiseltalensis* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
92	*Eodromus*† *agilis* (Meunier, 1915) (= *aeneocupreus* Pongrácz, 1935)	Pg(Eo-Geis) 48.6–40.4	[30,39,80]
93	*Eodromus*† *helopoides* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
94	*Eodromus*† *parvus* Haupt, 1956	Pg(Eo-Geis) 48.6–40.4	[30,39]
95	*Eodromus*† *punctatostriatus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
96	*Eodromus*† *punctatosulcatus* Pongrácz, 1935	Pg(Eo-Geis) 48.6–40.4	[30,39,81]
97	*Caryosoma*† *rugosum* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
98	*Parakeleusticus*† *postumus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
99	*Mimohelops*† *venosus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
100	*Anthracohelops*† *gigas* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
101	*Anthracohelops*† *minutus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
102	*Anthcarohelops*† *molassicus* (Heyden, 1865) Transferred from *Helops* to *Anthracohelops* Haupt, 1950 by Haupt [30]	Ng(Mi) 23–20.4	[22,30,39,70,71]
103	*Anthcarohelops*† *wetteravicus* (Heyden et Heyden, 1865) Transferred from *Helops* to *Anthracohelops* by Haupt [30]	Ng(Mi) 16.0–11.6	[22,30,39,70,71,75,82]
104	*Nesocyrtosoma antiquus* (Kaszab et Schawaller, 1984) (originally described is *Hesiodobates*; transferred to *Nesocyrtosoma* by Doyen and Poinar [38])	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
105	*Nesocyrtosoma antiquus* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
106	*Nesocyrtosoma celadonum* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]

Table 2. *Cont.*

No.	Taxon	Age and Site of Finding	Sources
107	*Nesocyrtosoma hadratum* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
108	*Nesocyrtosoma impensum* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
109	*Nesocyrtosoma phthanatum* Doyen et Poinar, 1994	Ng(Mi-Dom) 20.4–13.7	[38,39,57]
Tenebrionidae, family incertae sedis			
110	*Parapiophorus*† *nitidus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
111	*Eohelaeus*† *perpunctatus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
112	*Eohelaeus*† *sublaevis* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
113	*Eoallognosis*† *limbellus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
114	*Rhinohelaeites*† *longipes* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
115	*Rhinohelaeites*† *punctatulus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
116	*Rhinohelaeites*† *undulatus* Haupt, 1950	Pg(Eo-Geis) 48.6–40.4	[30,39]
117	*Tenebrionites*† *alatus* Cockerell, 1920	Pg(Eo-Flor) 37.2–33.9	[39,83]
118	*Tenebrionites*† *anglicus* Cockerell, 1920	Pg(Eo-Bour) 48.6–40.4	[39,83]
119	*Tenebrionites*† *inclinans* Cockerell, 1925	Pg(Pc) 66–55.8	[39,83]
120	*Protoplatycera*† *laticornis* Wickham, 1914	Pg(Eo-Flor) 37.2–33.9	[28,39]
121	*Tagenopsis*† *brevicornis* Heer, 1865	Ng(Mi) 12.7–11.6	[20,70,71,75]
122	*Eocallidium*† *rugulosum* Haupt, 1950, transferred from Cerambycidae to Tenebrionidae by Vitali [84]	Pg(Eo-Geis) 48.6–40.4	[30,85]
Coleoptera, family incertae sedis			
1	*Cistelites*† *insignis* Heer, 1865	Mz(Ju) 201.6–196.5	[20,59]
2	*Cistelites*† *sachalinensis* Heer, 1878	Mz(Cr) 85.8–84.9	[22,39,59,65]
3	*Cistelites*† *minor* Heer, 1883	Pg(Pc) 61.7–58.7	[22,39,65]
4	*Cistelites*† *punctulatus* Heer, 1883	Pg(Pc) 61.7–58.7	[22,39,65]
5	*Cistelites*† *longipes* (Hong, 1985) (*Procarabus*), transferred to *Cistelites* by Zhang [36]	Ng(Mi-Shan) 20.4–16	[35,36,39]
6	*Cistelites*† *spectabilis* Heer, 1847	Ng(Mi) 12.7–11.6	[19,39,65]
7	*"Helops" atticus* Redtenbacher in Unger, 1867	Ng(Mi-Kumi) 20.4–16	[39,44,84]

The following abbreviations (Table 1) are used for the various fossil deposits in Table 2, the figure, and the text below.

5. The Fossil Record of Major Tenebrionid Lineages

5.1. Tenebrionoid Branch.

5.1.1. Subfamily Alleculinae

The oldest known distinct representatives of Tenebrionoidea are from the Callovian/Oxfordian of the Middle/Late Jurassic, *Wuhua jurassica* (Wang et Zhang, 2011) [86] and *Praemordella martynovi* (Shchegoleva-Barovskaya, 1929) [87] and belong to the clade Mordellidae–Ripiphoridae of this superfamily [59]. *Archaeoripiphorus nuwa* (Hsiao et al., 2017) [88] from the same stage was originally described in Ripiphoridae but was later transferred to Tenebrionoidea familia incertae sedis [59]. Mordellid-ripiphorid beetles reach the largest proportion of the described taxa (32%) within Mesozoic Tenebrionoidea. Darkling beetles reach 11%, with the predominance of Alleculinae [59]. Such imbalances in the record seem to be a result of the fossilization: Ripiphoridae and Mordellidae are small beetles, common in Burmese amber, while much larger Mesozoic tenebrionids are known from Burmese amber by a single undescribed specimen; the majority of the Mesozoic tenebrionids were described from compression prints in a stone matrix. This is due to the different fossilization of bio-inclusions entering fossil resins and various types of compression in burials.

The oldest tenebrionid beetle *Cistelites insignis* (formally Alleculinae) from the Early Jurassic has an unclear position within Coleoptera, and the holotype of this species (print of single elytron) must be re-examined. The Middle/Late Jurassic *Jurallecula grossa* clearly belongs to the subfamily Alleculinae and, judging from its characters (preapical tarsomeres not bilobed), to the gonoderine branch of Alleculini [31]. Alleculinae are known by two described species from the Yixian Formation of the Lower Cretaceous [42,43], herewith *Calcarocistela kirejtshuki*, which belongs to gonoderine branch, and *Platycteniopus diversoculatus* has characters intermediate between those known in the alleculine and cteniopodine branches of the subfamily. All extant Cteniopodini associated with generative organs of Angiosperms and the age of *Platycteniopus* corresponds to the age of the early stages of the Angiosperm evolution. Probably, the origin of the tribe Cneniopodini should be dated to the Jurassic-Cretaceous border.

Many species of the formal genus *Cistelites* Heer, 1865, described from the Lower Jurassic of Switzerland (*C. insignis*), the Upper Cretaceous of Sakhalin (*C. sachalinensis*), the Lower Paleocene of Greenland (*C. minor* and *C. punctulatus*), the Middle Miocene of China (*C. longipes*) and the Upper Miocene of Germany (*C. spectabilis*) cannot be interpreted as possible close relatives, and this genus cannot be placed in the current classification due to its very sparse description. These taxa are not included in this review.

Numerous and diverse material on Alleculinae appears in the Cenozoic (Paleogene), especially in the Eocene Baltic and the Rovno amber, where mainly extant and one extinct (*Mycetocharoides* Schaufuss, 1888) genera are represented. The most diverse group among Baltic Alleculinae is the subtribe Gonoderina (tribe Alleculini). Two genera *Isomira* Mulsant, 1856 and *Gonodera* Mulsant, 1856 presented in the Recent fauna are registered in Baltic amber [52,54,65], herewith some extinct species of *Isomira* belong to the subgenera distributed in recent East Asia. This suggests that the most archaic representatives of this genus survived in the Palaearctic Asia and dispersed to the East Palaearctic, that is consistent with data on other families of beetles and plants [89,90]. The subtribe Alleculina, represented in Baltic amber by the genera *Allecula* Fabricius, 1801, *Mycetochara* Guérin-Méneville, 1827, and *Hymenalia* Mulsant, 1856, occur in the recent fauna and as well as the extinct genus *Mycetocharoides*, which only slightly differs from *Mycetochara*. The tribe Ctenipodini is known from Baltic amber by two extant genera, *Cteniopus* Solier, 1835, and *Cteniopinus* Seidlitz, 1896. The gonoderine taxa from the genera *Gonodera* and *Capnochroa* LeConte, 1862 [27,28], and the alleculine *Hymenophorus* Mulsant, 1851 [27], were described from the volcanic deposits of Florissant with a comparable age. It should be added that Doyen and Poinar [38] doubted the correctness of the Wickham's identifications. Only extant genera are known from the Neogene deposits [28], excluding the extinct genus *Sinocistela* Zhang, 1989, from the Miocene of China. *Sinocistela* clearly belongs to the tribe Cteniopodini because it has six exposed abdominal ventrites.

Based on the fossil record, the oldest tenebrionids are gonoderine comb-clawed beetles (tribe Alleculini, subtribe Gonoderina) with non-lamellar and non-bifurcated preapical tarsomeres. They are known from the Late Jurassic. However, taken into consideration their "modern" body, it can be assumed that this group probably originated earlier, perhaps in the Middle Jurassic.

Mesozoic gonoderine comb-clawed beetles are characterized by the morphological conservatism and slightly differ from the extant taxa of the subtribe Gonoderina (tribe Alleculini), with some particular adaptations, such as very long metatarsal spurs in *Calcarocistela*. Unlike Cteniopodini, many Alleculini feed on Cyanophita, Bryophita, or lichens growing on trunks of trees; only adults of some groups (for example, *Isomira*) switched to feeding on the generative organs of Dicotyledones, but their larvae develop in rotten wood, as do the larvae in most Alleculini [91,92].

The alleculine branch (subtribe Alleculina) appears in the fossil record only in the late Eocene, but that seems to be caused by a lack of material. Diverse taxa of this subtribe currently are widely distributed on all continents, and they most likely originated much earlier than indicated in the fossil record.

Separation of the alleculine and cteniopodine branches could have occurred at the Jurassic–Cretaceous border. Extant Cteniopodini feed on flowering plants: therefore, it is assumed that the appearance of the angiosperms promoted diversification of the subfamily.

5.1.2. Subfamily Tenebrioninae

Tenebrioninae is the largest and probably most diverse subfamily of darkling beetles in the Recent fauna. The oldest representative of this subfamily, *Alphotopsis initialis*, was found in the Lower Cretaceous Lagerstätte of Yixian, China [41]. This species, described from a well-preserved print, is very similar to extant taxa of the tribe Alphitobiini (in particular to *Alphitobius* Stephens, 1829) and has all characters typical for the subfamily, including intersegmental abdominal membranes, defensive glands, and open mesocoxal cavities with well-expressed trochantin. Only this particular species is known from the Mesozoic. Other tenebrionines appear in the fossil record with a long break only in the Middle Paleocene (the Thanetian in Menat, France). Taxa of Helopini and Opatrini are known from this deposit [44,45]. Representatives of these two tribes belong to extinct genera but have features of specialization as in the extant tenebrionids from these groups. For example, *Cryptohelops menaticus* is very similar to the extant genus *Stenohelops* sensu str., by having widened male protarsi, coarsely punctured prohypomera, cordiform pronotum, lacking wings, and epipleura not reaching the apex. Furthermore, the emargination on the inner side of the protibiae of *Cryptohelops menaticus* is characteristic also of some extant genera from the subtribe Helopina.

Paleosclerum pohli belongs to the specialized myrmecophilous group of the subtribe Sclerina, as some extant genera of the tribe Opatrini. One extinct opatrine genus, *Eupachypterus eocenicus* from the subtribe Neopachypterina is known from Lower Eocene Oise amber [46]. The extant taxa of this subtribe occur in the Indo-Malayan and Afrotropic regions, while others are distributed in transitional biogeographical areas of the Palaearctic.

All these findings (including taxa of Opatrini from distinct subtribes) indicate a much earlier Mesozoic diversification of various tribes of the subfamily Tenebrioninae.

The next Paleogene time period with diverse and multiple samples of Tenebrioninae is the late Eocene-early Oligocene, especially Baltic amber and Upper Eocene deposits of Florissant in the USA. Mainly extant genera from the tribes Bolithophagini, Pedinini, Triboliini, Ulomini, Helopini, Palorini are known in Baltic amber. Amber specimens listed by Klebs [29] are lost, and those taxa cannot be compared with extant ones. Helopini are represented by one abundant species *Stenohelops klebsi* [49]. This species is very similar to *Nalassus* spp. (subtribe Cylindrinotina) and was initially described in this genus. After the study of additional materials, it was transferred to the genus *Stenohelops* (subtribe Helopina) on the basis of the catomoid type of aedeagus [93,94], absence of grooves near the lower surface of eyes, double bead of abdominal ventrite 5, and widened male protarsi [52]. Palorini are represented in Baltic amber by two genera, the extinct *Vabole* Alekseev et Nabozhenko, 2015, and extant *Palorus* Mulsant, 1854. Eocene species of both taxa belong to the life form with flattened bodies, similar to those in the Gondvanian generic group *Platycotylus-Australopalorus* [47,48].

Four taxa of the subfamily Tenebrioninae were described from the Florissant deposits: two species of Opatrini, one from Bolithophagini and one from Amarygmini [24,28]. Both fossil species of Opatrini, *Ephalus adumbratus* and *Ulus minutus* (subtribe Opatrina) belong to the extant xeromorphic psammophilous genera with species occurring in inner-continental and marine supralittoral landscapes. *Proteleates centralis*, described in the tribe Bolithophagini, is very similar to the extant Neotropic genus *Eleates* Casey, 1886 (this genus was erroneously listed as *Proteleratus* and included to the tribe Blaptini by Kirejtshuk et al. [39]). Heyden and Heyden [18] erroneously placed *Bolitophagus vetustus* in this genus on the basis of two thin horns on the head. This species should be transferred to another genus of Bolitophagini, because this head character is typical for the extant Eastern Palaearctic and Indo-Malayan genus *Byrsax* Pascoe, 1860; some Neotropic *Megeleates* Casey, 1895, also have horns on the head. Wickham described *Meracantha lacustris* in the tribe Amarygmini; the second known species (extant) of this genus is distributed in North America and feeds on arboreal lichens.

Within the Palaeogene Tenebrionidae are some taxa with unclear positions (including members of the genera *Tenebrio* Linnaeus, 1758, *Bolitophagus* Illiger, 1798, and *Uloma* Dejean, 1821), from the Lower Eocene deposits of Canada (Whipsaw Creek) [23] and the Upper Oligocene deposits of Rott in Germany [16–18], which were only briefly described and poorly illustrated. Only the recent genera occur in the Neogene. The most reliable information relates to taxa from the genera *Wattius* Kaszab, 1982 (Toxicini), *Rhipidandrus* LeConte, 1862 (Bolithophagini), *Cymatothes* Dejean, 1834 (Amarygmini), and *Hypogena* Dejean, 1834 (Triboliini), described from the Miocene Dominican amber [38]. The majority of mentioned genera are spread in the Neotropics and partly in the Nearctic regions, with the exception of *Rhipidandrus*, species of which are known from all tropical areas of the World.

Within the described Neogene darkling beetles, the Miocene Helopini are the most diverse, but the tribal position of these taxa is very doubtful. All these species were described in the genus *Helops* sensu lato, which in the 19th century contained the most current helopin genera and many unclear genera from different subfamilies of tenebrionid beetles. It is impossible to clarify the taxonomic position of these taxa without examining the type specimens. Comments on these species are given below:

[*Helops*] *atticus* Redtenbacher in Ungern, 1867 (Ng(Mi-Kumi) 20.4–16). This species was described on the basis of the print of the right elytron and compared with extant *Entomogonus peyronis* (Reiche, 1861) and *Erionura gigantea* (Kraatz, 1862). The high-quality image in the original description does not give any reason to clearly attribute this print to any subfamily of Tenebrionidae. As a result, this species is regarded as Coleoptera, family incertae sedis.

[*Helops*] *meissneri* Heer, 1847 (Tafel V, Figure 9) (Ng(Mi)12.7–11.6). This print, as described in detail, can belong to *Helops* sensu str. Its most peculiar character is the distinct deflected lateral margin of elytra. Its head is very poorly preserved and cannot be used for diagnostics. O. Heer mentioned in the original description that its elytra are similar to some *Carabus* Linnaeus, 1758, but the clearly-expressed full elytral striae indicate the possible position of this species within the genus *Helops*. Unfortunately, the image in the original description is not informative.

5.1.3. Subfamily Stenochiinae

The oldest representative of the subfamily Stenochiinae is known from the early Paleocene of Greenland (Pg(Pc) 61.7–58.7): *Pseudohelops groenlandicus* (originally *Helops molassicus* Heer, 1883). Haupt [30] compared this genus and species with the Eocene species of *Anthracohelops* on the basis of a similarity in the metallic shine of its elytra but contraposed both genera in the structure of elytral striae. Other Stenochiinae are known from the Middle Eocene of Germany (Pg(Eo-Geis) 48.6–40.4), where they were hugely diverse [30]. Haupt described several taxa in 1950 [30]: *Pyrochalcaspis* (one species), *Eodromus* (five species), *Caryosoma* (one species), *Paraceleusticus* (one species), *Anthracohelops* (four species), *Mimohelops* (one species) and *Pseudohelops* (one species). He divided all these genera by the structure of pronotum and the elytral sculpture. The first two can be compared with the extant species of the Neotropic genus *Hegemona* Laporte, 1840 (Cnodalonini), which also have fusiform convex elytra with very deeply impressed strial furrows. The genus *Eodromus* was compared by Haupt with extant representatives of the Neotropic genus *Camaria* Lepeletier and Audinet-Serville, 1828. However, *Eodromus* distinctly differs from *Camaria* and allied Neotropic genera (*Mylaris* Pallas, 1781, *Taphrosoma* Kirsch, 1866, etc.) in the absence of humeral angles (while the mentioned extant genera have clear humeral angles and callosity indicating the ability to fly). *Eodromus* can be compared with recent *Hegemona*, which are also wingless and have very similar elytral sculpture. Another genus, *Cariosoma* Haupt, 1950, "close" (according to Haupt) to *Eodromus*, has strongly sculptured elytra with elongate tubercles, similar to those in the Indo-Malayan taxa of the tribe Cnodalonini (*Morphostenophanes* Pic, 1925, and allied genera). *Parakeleusticus postumulus* is very similar to the recent *Hegemona resplendens* Laporte, 1840, from Southern Mexico. The taxonomic position of other mentioned genera of the subfamily Stenochiinae remain unclear, although Haupt compared them with the recent *Camaria* (Cnodalonini).

Thus, in the early Eocene of Geiseltal (Pg(Eo-Geis)48.6–40.4) the thermophilic and humid adapted species of the subfamily Stenochiinae, similar to those from Recent Neotropic and Indo-Malayan taxa, were well represented. This, as in the case of the Coleoptera composition in the earliest Eocene amber Oise, could be just at the beginning of the transition from the climatic thermo-era to cryo-era, from the thermal maximum in the Paleocene–Eocene to the global trend of climate cooling in the Middle Eocene–late Oligocene [95].

Other fossil Stenochiinae, all from the extant genus *Nesocyrtosoma* Marcuzzi, 1976, are known only from Neogene Dominican amber [38].

5.1.4. Subfamily Diaperinae

Diaperinae are poorly represented in the fossil record. This feature probably relates to their secretive lifestyle in natural landscapes, such as inside tunnels of bark beetles (Hypophlaeini), in the litter of trees and shrubs (many Gnathidini), in tree mushrooms, and under the bark (Diaperini, Scaphidemini).

The oldest extinct genus of Diaperinae was found in the Paleocene of Menat (Pg(Pc)61–56) and belongs to the tribe Scaphidemini (Nabozhenko & Kirejtshuk, in litt.).

Ceropria messelense was described from the early Eocene of Germany (Pg(Eo-Mess)48.6–40.4), although this genus was determined by the author with doubts [80]. Extant representatives of this genus are widespread in the Indo-Malayan Region.

Some Diaperinae were listed from the late Eocene to early Oligocene: Pg(Eo-BA)37.2–33.9 and Pg(Eo-Flor) 37.2–33.9. All of them belong to extant genera of the tribe Diaperini: two species of *Platydema* Laporte and Brullé, 1831, from Florissant [27], and one species of *Pentaphyllus* Dejean, 1821, [39] from Baltic Amber. The recent representatives of the first genus are widely distributed in the Palaearctic, Nearctic, Indo-Malayan, Afrotropic, and Neotropic regions. *Pentaphyllus* occurs in the same biogeographical regions, except Neotropic.

Miocene Dominican amber is characterized by the slightly more diverse composition of diaperines. Only the species from the extant widely distributed groups were listed in this source: Hypophlaeini (*Corticeus* Piller and Mitterpacher, 1783, worldwide distribution), Gnathidini (*Tyrtaeus* Champion, 1913, Australia, Neotropic, Nearctic), Diaperini (*Neomida* Latreille, 1829, all biogeographical regions, except for Australia; *Liodema* Horn, 1870, Nearctic, Neotropic) [38,56,57].

5.2. Pimelioid Branch

Subfamily Pimeliinae

Taxa of pimeliine branches are poorly represented in the fossil record because they probably occurred, as did the Recent members of this tribe, mostly in arid biomes (deserts and semideserts), and they would rarely be deposited in tree resin or compression lacustine burials. However, even single records are of great interest because they can help to analyze the diversification of pimeliine tribes, as well as to reconstruct paleo landscapes.

In the paleontological record, only extant tribes of Pimeliinae are presented (Asidini and Stenosini). Fossil species of tribe Asidini were found in the deposits of Florissant (Pg(Eo-Flor) 37.2–33.9) (*Pelecyphorus* (*Stenosides*) *primus*) [27] and in Baltic amber (*Asida* (*Planasida*) *groehni*) [53]. Both species belong to extant subgenera and undoubtedly demonstrate the earlier (possibly, early Eocene or late Paleocene) diversification of these groups. The finding of fossil *Asida groehni* in Baltic amber permits a more critical look at various reconstructions of the Baltic amber forest, in which the presence of xerophytic landscapes was not assumed in previous interpretations, and also the taphonomic reasons and selectivity of the amber fauna were not always taken into account [96,97]. Meanwhile, the Palaearctic genera of this tribe are xeromorphic (closed mouthparts without membranous surfaces, developed subelytral cavity, etc.) and include species of *Asida* Latreille, 1802, and allied genera that inhabit dry landscapes in arid Mediterranean woodlands, steppes, and semideserts. At least arid woodlands undoubtedly existed in the late Eocene landscapes of the Paleo-Eurasia.

Another fossil representative of the subfamily Pimeliinae belongs to the tribe Stenosini, which includes the myrmecophilous species, sporadically occurring in the Recent New World and widespread in the Recent Old World, mainly in the Palaearctic and the dry subtropics of the Indo-Malayan Region. *Miostenosis lacordairei*, described from the Eocene Florissant deposits on the basis of well-preserved print [27], is externally similar to the Palaearctic *Stenosis* Herbst, 1799. A distinctive feature of *Miostenosis* Wickham, 1913 is large round eyes, not characteristic of Stenosini, which have narrow, partly, or completely divided eyes, sometimes oval dorsally (some *Stenosis*). The taxonomic position of this extinct species is still unclear.

A single Neogene fossil representative of the extant genus of the tribe Edrotini, *Trientoma hascens*, was described from Miocene Dominican amber [38]. The extant species of this genus are distributed in the West-Indies and often occur in coastal dry woodlands or dry subtropic forests.

5.3. Lagrioid Branch

5.3.1. Subfamily Lagriinae

The subfamily is first known in the fossil record in Cretaceous Burmese amber (yet undescribed species of the tribe Lagriini: Statirina from Burmese amber). After a long time gap in the fossil record the lagriine taxa appear in the Middle Paleogene (most diverse in Eocene Baltic amber), genera from which four tribes were listed: *Laena* Dejean, 1821 (Laenini), *Gonialaena* (Gonialaenini), *Luprops* Hope, 1833 (Lupropini), *Lagria* Fabricius, 1775, and *Statira* Lepeletier and Audinet-Serville, 1828 (Lagriini), and also extinct *Yantaroxenos* (Belopini) [39,50,51]. Two from six described genera (33%) are extinct (*Gonialaena*, *Yantaroxenos*).

The genus *Yantaroxenos* is most similar to the Neotropic *Rhypasma* Pascoe, 1862, which indicates ancient connections of the Early and Middle Paleogene faunas of Coleoptera of different paleo continents [29,32]. Records of many taxa of the mainly tropic subfamily Stenochiinae in early Eocene deposits of Geiseltal (Pg(Eo-Geis) 48.6–40.4) [30] also support this assumption.

The separate tribe Gonialaenini was erected for the genus *Gonialaena* because it combines some characters of the tribes Laenini, Goniaderini, Lupropini, and Lagriini and, possibly, represents a Mesozoic relic that survived until the late Eocene [51].

In Neogene Dominican amber are the only known fossil species of *Lorelus* Sharp, 1876, and *Statira* [38]. The extant taxa of the first genus are widely distributed in the New World; however, extant species of *Statira* occur in the Indo-Malayan, Nearctic, and Neotropic regions.

5.3.2. Subfamily Nilioninae

These unusual darkling beetles were interpreted within the Lagrioid branch of Tenebrionidae [1]. All extant taxa of the subfamily are Neotropic. The only extinct species *Nilio dominicanum* was described from the Miocene Dominican amber [98]. The species was originally described as *dominicana* but should be corrected to *dominicanum* according to the neuter generic gender. The extant species of Nilioninae feed and develop on lichens [1,99].

6. The Fossil Record of Tenebrionidae in Evolutionary Reconstructions

The conclusions regarding fossil Tenebrionidae are primarily assumptions based on incomplete material rather than postulates.

In the current evolutionary scenario using molecular dating and diversification analyses, Kergoat et al. [14] suggested that Tenebrionidae originated after the Triassic-Jurassic mass extinction, and diversification of the major branches of Tenebrionidae proceeded in the period of Pangaean and Gondwanan breakups. These authors established that arid-adapted darkling beetles (mostly

Pimeliinae) diversified earlier (in the Middle-Late Jurassic), while the humid-adapted tenebrionids (Tenebrioninae, Diaperinae, Stenochiinae) diversified much later, in the early and late Cretaceous (Alleculinae).

Generally, the fossil record supports this view (Figure 1), but some discrepancies can be found. Based on the record of Middle/Late Jurassic *Jurallecula grossa* (Mz(Ju) 164.7–155.7), L. Medvedev [31] was the first who assumed (long before modern studies), that Tenebrionidae originated in the early Jurassic or slightly earlier. So, his estimated time of the origin of darkling beetles does not contradict Kergoat et al. [14]. Despite the lack of paleontological evidence, the presumably Jurassic diversification of the pimelioid branch as assumed by Matthews et al. [1] and Kergoat et al. [14] can be supported. It can also be assumed that the pimeliine tenebrionids during the Jurassic were diversified and produced main separated phyletic branches because, among all extant representatives of the largest subfamily Pimeliinae and the small Kuhitangiinae, mesophilic humid-adapted groups are absent.

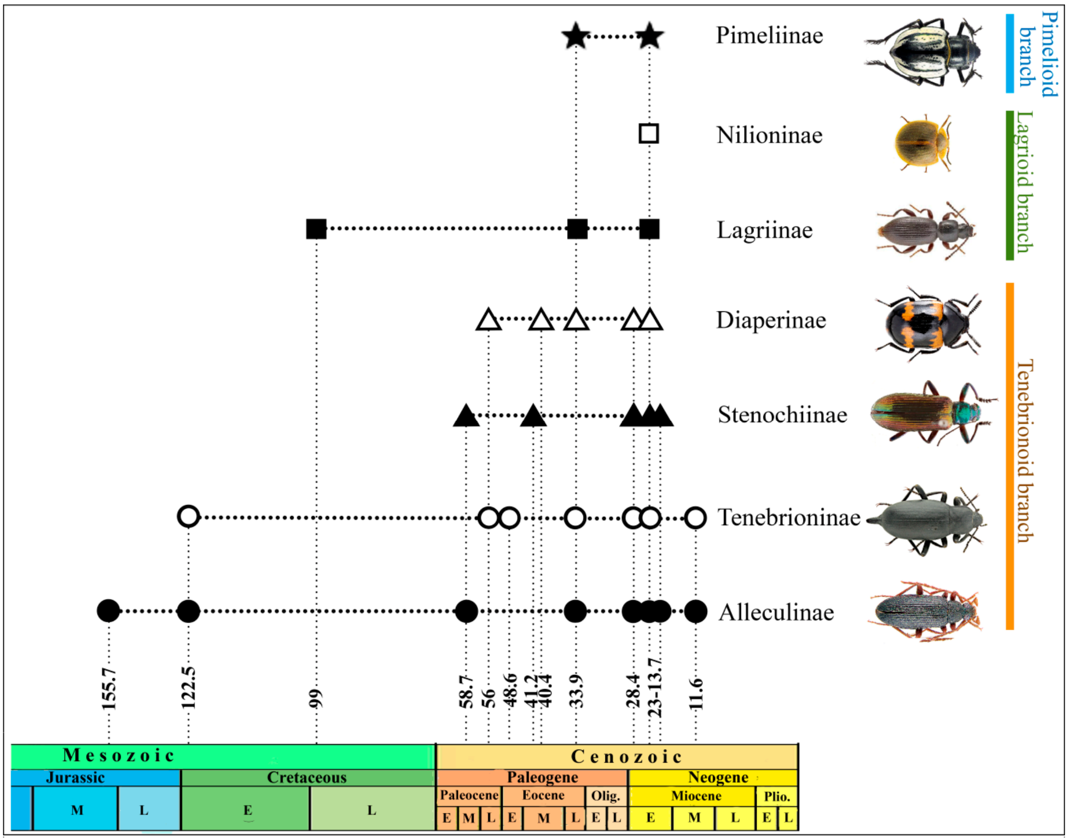

Figure 1. Tenebrionidae in the fossil records. Numbers show minimal age of fossils.

The oldest Jurassic and Jurassic-Cretaceous darkling beetles of the tenebrionine lineage belong to humid-adapted groups from the extant tribes Alleculini, Ctenopodiini (Alleculinae), and Alphitobiini (Tenebrioninae) (Figure 1). Thus, Paleontological evidence supports a hypothesis that the differentiation of the family started at least in the Middle Jurassic, regardless of whether the ancestral forms of Tenebrionidae were xerophilic or mesophilic (Figure 1). In this case, paleontological evidence contradicts the scenario suggested by Kergoat with coauthors [14].

A more or less distinct time interval can be established only for the origin of the tribe Cteniopodini. The oldest genus of this tribe, *Platycteniopus* (Mz(Cr) 125.5–122.5), combines both the features of gonoderine ancestors and the "new" cteniopodine characters, which are explained by the change of trophic specialization of all representatives of this tribe to feeding on generative organs of angiosperms. This is the only known case of the direct impact of early angiosperms on the evolution of darkling beetles. In this case, we support the opinion of Kergoat with co-authors [14] about the insignificant impact of angiosperms on the diversification of tenebrionids, contrary to Yu et al. [64], who indicated the origin of Tenebrionidae in the Cretaceous (near 120 Ma) and an important role of angiosperms in their evolution.

The main contradiction is a discrepancy between the fossil record, morphological conclusions and evolutionary scenarios. According to many morphological works and phylogenetic reconstructions [1,3,6–11], the hypothetical ancestor of tenebrionid beetles had the characters typical of the lagrioid branch and archaic Zolodininae (tentatively pimelioid branch). However, the oldest Tenebrionidae belong to the tenebrionoid lineage and only partly fit the 'lagriine' features (Table 3).

Table 3. Comparison of a hypothetical ancestor of darkling beetles [10] and latest Jurassic and early Cretaceous Tenebrionidae [31,41–43] (matching characters are marked with a grey background).

No.	Hypothetical Lagrioid Ancestor *	Oldest Fossil Tenebrionoid Darkling Beetle (Alleculinae)
1	Simple trichoid antennal sensilla	Mixed, compound, and simple trichoid antennal sensilla
2	Longitudinal labrum	Transverse labrum
3	Internally and probably externally open procoxal cavities	Procoxal cavities closed externally and (at least in extant taxa) internally
4	Elytra with ten full striae	Elytra with nine striae and short scutellary striola
5	Wings with medial fleck	Unknown for fossil species. Extant Alleculinae without median fleck, and Tenebrioninae without or with
6	Groove along the outside edges of the abdominal ventrites, into which the elytral edges could fit to produce a sealed subelytral cavity	
7	Ovipositor with four coxites and terminal styli	Ovipositor with four coxites and lateral styli
8	Female genital tract with the primary bursa copulatrix and without spermatheca	Alleculinae: unvisible in fossils Extant taxa: female genital tract with primary or secondary bursa copulatrix and without spermatheca
		Alphitobiini: unvisible in fossils Extant taxa: female genital tract without bursa copilatrix, with spermatheca
9	Aedeagus without alae (extensions of the apical piece)	Aedeagus with alae (at least in *Platycteniopus diversoculatus*)
10	Defensive glands are absent	Defensive glands are presented (well visible intersegmental membranes between abdominal ventrites 3–5)

* The ancestor is most closely related to the extant Belopini of the lagrioid branch and Zolodininae, tentatively in the Pimeloid branch [10] and probably Kuhitangiinae of the pimelioid branch [13]

Thus, only two characters fit (character eight only partly fits) the hypothetical ancestor of darkling beetles. One additional dual character in the hypothetical ancestor is the open or closed mesocoxal cavity. Zolodininae, the most primitive Tenebrionidae that is similar to the hypothetical ancestor, have open mesocoxal cavities, but Belopini and Kuhitangiinae have closed ones. Matthews and Bouchard [10] (p. 35) assumed that "tenebrionoids would have branched off very soon thereafter" because Palorini of the tenebrionoid branch have many of the mentioned "ancestral" characters. In general, this hypothesis is supported by the fossil record, and also, it can be assumed that three main lineages of Tenebrionidae were branched during a short time period.

On the other hand, the oldest fossil Tenebrionidae has many characters (1–5,7,10), which are currently interpreted as derived [1,10]. This discrepancy can be explained by gaps in the fossil record (especially in Jurassic deposits) and the earlier origin of Tenebrionidae, in Early Jurassic, as assumed by L. Medvedev [31] and Kergoat et al. [14]. In any case, taking into account the grounded monophyly of Tenebrionidae, the basal diversification (branching of the main lineages) of this family started at the earliest stages of the evolution of the darkling beetles.

7. Conclusions

The family Tenebrionidae is represented in the fossil record with 122 species, 78 genera (including 29 extinct genera) from seven subfamilies of three main branches in the time span of 201–11.6 Ma. This includes the lagrioid branch (Lagriinae, Nilioninae), pimelioid branch (Pimeliinae), and tenebrioid branch (Alleculinae, Tenebrioninae, Diaperinae, Stenochiinae). The most diverse records are reported in the Paleogene, Eocene (Geiseltal Halle, Baltic Amber, Florissant), and Miocene Dominican Amber. The oldest known distinct Mesozoic darkling beetles are from the Middle/Late Jurassic of Karatau (Alleculinae) and early Cretaceous of Yixian (Alleculinae and Tenebrioninae).

Darkling beetles of the tenebrionoid branch are the most diverse in the fossil record: Alleculinae: 30 species (since Middle Jurassic in the fossil record); Tenebrioninae: 28 species (since early Cretaceous in the fossil record); Stenochiinae: 21 species (since Middle Paleocene in the fossil record); Diaperinae: 15 species (since Middle Paleocene in the fossil record); lagrioid branch: 14 species: Lagriinae: 13 species, including an undescribed one (since late Cretaceous in the fossil record); Nilioninae: one species (since early Miocene in the fossil record).

Paleontological evidence partly suggests that the following evolutionary scenarios of Tenebrionidae occurred as indicated by Kergoat with co-authors [14]: (1) angiosperms had an insignificant impact on the diversification of tenebrionids, with the exception of diversification of the pimelioid branch during the Late Jurassic; (2) paleontological evidence supports the differentiation of the family at least by the Middle Jurassic, whether the ancestral forms of Tenebrionidae were xerophilic or mesophilic. Discrepancies between the hypothetical lagrioid ancestor of Tenebrionidae and the oldest known tenebrionoid fossils are possibly related to gaps in the fossil record.

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