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Coleoptera from the middle-upper Eocene European ambers: generic composition, zoogeography and climatic implications

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Abstract

The paper contains a review of coleopteran genera known from Baltic, Bitterfeld and Rovno amber localities. Altogether 420 genera (191 extinct and 229 extant) from 78 families are listed from these three Lagerstätten (as of 7 March 2017). The listed beetles were analyzed zoogeographically and distributional maps for 72 genera were compiled. One-quarter (56) of the genera that have survived since the Eocene have cosmopolitan ranges at present; 35 extant genera have been extripated from the Palaearctic since the Eocene. Approximately 40% of beetle genera from the middle-upper Eocene European ambers can be encountered in the wild in present-day Europe, while 5 of these genera are supposed to be European relict endemics originating in Fennosarmatia. The general similarity of the Baltic amber (*s.l.*) beetle assemblage to modern south Palaearctic fauna is the strongest, the Nearctic elements are more numerous in the middle-upper Eocene European ambers than the Oriental taxa. The simplified Mutual Climatic Range (MCR) method was used for palaeoclimate reconstruction based on fossil beetles. The coleopteran assemblage of Baltic amber is interpreted as indicative of warm temperate, humid, equable climate with reduced thermal seasonality [annual average temperatures range from +10–20˚C; mean of the coldest month temperatures around +10˚C; mean of the hottest month temperature around +20–24˚C; annual precipitation around 750–1500 mm]. The primary importance of high humidity for existence of the Eocene biota is pointed out.

Key words: Paleogene, Neogene, beetles, extant genera, range overlaps, palaeoclimate reconstruction, ecological zoogeography

Работа посвящена обзору родов жесткокрылых балтийского, биттерфельдского и ровенского янтаря. По состоянию на 7 марта 2017 года в приводимом списке жуков этих трех лагерштетов 420 родов (191 вымерший и 229 современных) из 78 семейств отряда. Указанные таксоны родового уровня проанализированы зоогеографически, для 72 из них составлены карты современных ареалов. Четверть жуков, известных из сукцинита (56 родов), в настоящее время—космополиты, 35 современных родов полностью вымерли в Палеарктическом регионе. Около 40% жуков из европейских янтарей среднего-позднего эоцена обитают в современной Европе, 5 родов—предположительно реликтовые эндемики этой территории, возникшие в Фенносарматии. Сходство фаунистического комплекса жуков сукцинита с современной фауной южной Палеарктики наиболее сильно; доля современных неарктических элементов в европейском средне- поздне-эоценовом янтаре больше, нежели доля представителей Индо-Малайского региона. Проведена реконструкция палеоклимата на основании современных представителей родов жуков эоценового янтаря по упрощенной методике перекрывающихся ареалов. Состав жесткокрылых сукцинита интерпретирован как указание на умеренно-субтропический гумидный климат без выраженных сезонных перепадов температур: значение среднегодовой температуры в пределах +10–20˚C; средняя температура самого холодного месяца предположительно около +10˚C; значение температуры самого жаркого месяца приблизительно +20–24˚C; годовое количество осадков 750–1500 мм. Подчеркивается исключительное значение высокой влажности климата для существования эоценовой биоты.

Ключевые слова: палеоген, неоген, жуки, современные роды, перекрывание ареалов, реконструкция палеоклимата, экологическая зоогеография

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Introduction

The inclusions within Baltic amber are especially important for tracing the evolutionary history of modern genera and also for elucidating the diversity of terrestrial palaeoecosystems. The beetle inclusions in Baltic amber and in the similarly aged (middle or late Eocene succinites) analogs from the Ukraine and Germany are currently attracting much attention and have been intensively studied with descriptions of new taxa in various families. Different authors have published research on beetles from Baltic amber, largely focused on new species and genera descriptions. The review of beetle species (Coleoptera) described from Baltic amber was published three years ago (Alekseev 2013), but that list consisting of 434 described species needs significant additions now. Since that publication, many new taxa have been described and the taxonomic status of several others has been corrected. The spectrum of families known in Baltic amber has significantly broadened and, apart from the awaited first descriptions in Bostrichidae, Corylophidae, Histeridae, Monotomidae, Salpingidae, Smicripidae, Tetratomidae and Zopheridae, families such as Ischaliidae (Alekseev & Telnov 2016), Jacobsoniidae (Cai *et al.* 2016), Omalisidae (Kirejtshuk & Kovalev 2015), and Passandridae (Bukejs, Alekseev *et al.* 2016) have recently been reported from succinite, and are added to the current list. The synoptic list of the described from Bitterfeld amber beetles was provided earlier (Bukejs, Biondi *et al.* 2016).

Despite the considerable efforts devoted to the definition of the taxonomic composition of Baltic amber beetles, their biogeographical and palaeoclimatical features have received only limited attention. Comprehensive information about trophic peculiarities of beetles included in Baltic amber was presented by Alekseev & Alekseev (2016). The zoogeographical data concerning separate groups of beetles can be found in various revisional descriptions of new taxa (e.g., Muona 1993; Kolibáč 1998; etc.). Aside from these works, several generalized zoogeographical treatments concerning Baltic amber were made by Ander (1942), general conclusions about all insects of the Paleogene period were formulated by Zherikhin (1970) for the first time and the ratio of tropical and Holarctic species for taxa, such as ants in late Eocene ambers, have recently been analyzed (Perkovsky 2016 and references therein).

A zoogeographical and comparative climatic analysis of the various beetle genera found in the succinites of Europe has been never made. A range of hypotheses about climate in the forest that produced Baltic amber can be found in different sources, with variable support and merits (e.g., Andrée 1951; Larsson 1978; Poinar 1992; Weitschat & Wichard 1998). Based on beetle species composition, detailed climatic and landscape reconstructions have been made for other regions and time intervals, such as the Quaternary of the southern part of the West-Siberian Plain (Zinovyev *et al*. 2016) or the Cretaceous Spanish and French ambers (Peris *et al*. 2016) . The Mutual Climatic Range (MCR) method, which reconstructs climatic conditions associated with a fossil beetle assemblage by comparison to Recent species, has been applied successfully to different Quaternary deposits (e.g., Huppert and Solow 2004; Elias and Matthews 2014). This technique may allow us to investigate conditions in the Eocene amber-producing forests of Europe as well.

The purpose of this study is to carry out zoogeographical analysis and climatic interpretation of the Eocene coleopteran assemblage of the middle-upper Eocene European amber (Baltic, Bitterfeld, and Rovno deposits). The work performed includes four main steps: (1) summarizing of the data available and compiling an updated generic list of beetles known from these amber-bearing deposits; (2) synthesis of up-to-date distributional information for surviving Eocene genera and representative mapping of their modern ranges; (3) biogeographical grouping of recent distribution areas of genera with a minimum Eocene age; (4) analysis of the present-day climates preferred by the surviving Eocene beetles and the extrapolation of these conditions for the territory of the Baltic amber forest. Topics such as the possible migration routes of beetle genera, and landscape reconstructions are also discussed herein.

Material and methods

The beetles described from Rovno/Ukrainian amber (localized in north-western Ukraine and south-western Belarus), and from Bitterfeld/Saxonian amber (localized in Bitterfeld-Wolfen, in Sachsen-Anhalt, Germany), are united and counted together with taxa from "authentic" Baltic amber (originating from the seacoasts of Denmark, northern Germany, Poland, the Kaliningrad region of Russia, Lithuania, and Latvia) in the present paper. These ambers are not distinctly different (or, more exactly, not reliably compared to one another at present) in terms of their included beetle content, and the deposits share a similar temporal and geographic source, so they are generally treated as one "amber type" in this paper [called "Baltic amber (*s.l.*)" or "succinite"]. There are different standpoints concerning the topic of European amber differentiation (Hoffeins & Hoffeins 2003; Perkovsky *et al.* 2007; Szwedo & Sontag 2009, 2013; Vitali 2011; Penney & Preziosi 2014; Wolfe *et al.* 2016), but a full discussion of this topic is beyond the scope of the present paper. The geographical differentiation of Baltic amber *s.l.* into Jutland (Danish) amber, amber of the Gdańsk Gulf and Sambian amber from Yantarny, appears to be somewhat artificial, and such divisions are at a much finer scale than the geographic comparisons made in the present study. All of these amber subunits were united in this paper and considered to be originated from territories of Fennosarmatia [Russoscandia] and its nearest vicinities.

The compiled checklist of the coleopteran genera from the middle-upper Eocene European ambers includes the most accurate reports only. The list consists of genera with described species (except for some equivocal old descriptions, see below), and of generic reports with a high degree of certainty (i.e., those that come from modern papers). The available modern generic concepts, generic revisions, and data on taxon distributions were used in this work (Nikitsky & Below 1982; Peacock 1987; Ślipiński 1987; Schawaller 1983, 2005; Newton & Chandler 1989; Ślipiński *et al.* 1989; Bellamy 1990; Muona 1991; Nikitsky 1992, 2016; Bellés 1996; Kolibáč 1997; 1998, 2013; Newton & Franz 1998; Schöller 2002; Bousquet 2003a, 2003b; Medvedev 2003; Háva 2004; Nikitsky 2004; Toskina 2004; Miller 2005; Costa *et al.* 2006; Ferrer *et al.* 2007; Wanat 2007; Alonso-Zarazaga & Lyal 2009; Růžička & Pütz 2009; Schimmel & Tarnawski 2010; Hájek 2010; Alonso-Zarazaga *et al.* 2011; Dudko 2011; Cline *et al.* 2014; Vitali 2014; Zahradník & Háva 2014; Háva 2015; Legalov 2015, 2016a; Węgrzynowicz 2015; Gimmel & Bocakova 2015; Ivie *et al.* 2016; Kirejtshuk, Nel *et al.* 2016; Vitali & Daamgard 2016; Zanetti *et al.* 2016; Reike (pers.comm.); Jäch (pers.comm.). The recently proposed synonymies for fossil genera (Nagel 1987; Kolibáč 1997; Kolibáč 1998; Klausnitzer 2003; Vitali 2006a, 2006b, 2009; Reike 2012; Telnov 2012; Bukejs *et al.* 2012; Kazantsev 2013; Reike *et al.* 2013; Bukejs *et al.* 2015; Legalov 2015, 2016b; Ortuño and Arillo 2015; Bukejs & Schmitt 2016; Batelka 2017) were used as well. The division of the present-day Earth into six major zoogeographical units (Nearctic, Neotropical, Palaearctic, Afrotropical, Oriental and Australian) was applied. The limits of the biogeographical regions are defined in general accordance with the "Catalogue of Palaearctic Coleoptera" (Löbl and Smetana 2003), in which the Palaearctic area includes South China, Northern India, Nepal and Bhutan for example.

Ten recent genera from old descriptions (*Airaphilus*, *Anobium*, *Apion*, *Bothrideres*, *Chrysomela*, *Clidicus*, *Larinus, Ptomaphagus*, *Spondylis*, and *Trechoblemus*) and one unclear fossil (*Criocerina* Germar, 1813) were considered doubtful and are not counted in updated list. The independent "fossil" status of the genera *Archaeoscraptia* Abdullah, 1964 and *Palaeoscraptia* Abdullah, 1964 should also be considered doubtful, but these taxa are listed according to the author's interpretation. Additionally, the following 21 reliably reported genera (without described species) were added to the list: *Stenaesthetus* Sharp, 1874; *Octavius* Fauvel, 1873; *Euaesthetus* Gravenhorst, 1806 (Puthz 2008); *Chevrolatia* Jacquelin du Val, 1850; *Cephennodes* Reitter, 1884 (Jałoszyński & Kubisz 2016); *Rhagomicrus* Fleutiaux, 1902; *Microrhagus* Dejean, 1833; *Arisus* Bonvouloir, 1871; *Poecilochrus* Bonvouloir, 1871; *Hemiopsida* MacLeay, 1872; *Fornax* Laporte de Castelnau, 1835; *Asiocnemis* Mamaev, 1976; *Dromeolus* Kiesenwetter, 1858 (Muona 1993); *Brachypsectra* LeConte et Horn, 1883 (Klausnitzer 2009); *Petalium* LeConte, 1861 (Alekseev 2014); *Aplocnemus* Stephens, 1830; *Xamerpus* Fairmaire 1886 (Majer 1998); *Canifa* Le Conte, 1866 (Kubisz 2001); *Prostomis* Latreille, 1825 (Schawaller 2003); *Holoparamecus* Curtis, 1833 (Kubisz 2000; Rücker 2012); *Oedemera* Olivier, 1789 (Grünemaier 2016). The specimens of the following recent genera are currently under study and will be described or reported in the near future: *Palorus* Mulsant, 1854; *Seidlitzella* Jakobson, 1915; *Symbiotes* Redtenbacher, 1849; *Trichodesma* LeConte, 1861; *Trochoideus* Westwood, 1833. These taxa were included in the list and analysis too (pers. obs.) but are listed without species numbers.

The large list of beetle genera from the former University of Königsberg (Albertina) is presented by Klebs (1910). Beyond all doubt, this excellent paper is the most comprehensive Baltic amber beetle list of the XX century. Unfortunately, the applied in this paper generic systematics is generally out-of-date and cannot be blindly used without re-study of specimens, which are lost or scattered in different European amber collections. In current research, the taxa from the paper of Klebs (1910) were not listed in order to avoid any errors.

Only the extant genera reported from the middle-upper Eocene European ambers (and therefore of at least Eocene age) were zoogeographically analyzed. Each genus is considered to be monophyletic (representing one lineage), with a single point and time of origin. It is assumed that each genus is associated with a specified climate and food sources, and that such ecological connections and requirements are more or less constant (conforming to the actualisic concept). A genus has the simplified six-stage model of existence that follows the pattern of: origin—gradual distribution—more or less stabile existence in a wide territory with oscillations of distributional area—gradual contraction of range—formation of isolated relict populations in the most appropriate climatic regions—extinction. The hypothetical formation and diversity of the beetle fauna and its gradual distribution before and during Eocene and the absence (Smith & Marcot 2015) of unusually rapid extinction on the Cretaceous-Paleogene boundary is supposed. The present-day distributional areas of the genera with minimally Eocene age are formed mainly by reduction of previous ranges (stages 3–6 of the model).

The current catalogue was compiled based on published literature sources. The genera within each family are listed alphabetically and arranged in families according Bouchard *et al*. (2011) and Robertson *et al*. (2015). The family Dryophthoridae was placed in Curculionidae as subfamily Dryophthoridae according to Anderson & Marvaldi (2014). The original descriptions are not cited for the sake of brevity. The data for each genus is compiled according following formula:

"Genus name [succinite locality—the number of described species from the studied Eocene ambers]; fossil/recent state of genus: distribution for extant genera. Figure of distribution (for the 72 extant genera only)".

Three main localities of succinite were recognized in this study, and abbreviated to the following: BaA—true Baltic amber, BiA—Bitterfeld amber, RoA—Rovno amber. The locality of only each beetle holotype was taken in account. The criterion of presence/absence is used herein (*i.e.,* the note "Palaearctic" designates the genus occurring in Palaearctic region even if the range here is very restricted). The term "cosmopolitan" is used for globally distributed genera occurring in all six major zoogeographical realms. More specific notes concerning distributional details are made in parenthesis (*e.g.*"non-European") for some genera. Information about present-day occurrence in Madagascar is separately noted, but in the general analysis this region is considered part of the Afrotropical realm. The abbreviations for "northern" is N, "southern"—S, "western"—W, "eastern"—E.

The modern distribution of the extant genera known from Eocene ambers and comparison with modern climatic pattern of the Earth was made in order to find a link between beetle distribution and climate. Two modern climatic classifications were used: the effective classification of Köppen-Geiger (maps according to Peel *et al.* 2007) and the integrative classification by Lauer-Frankenberg, taken from standard Diercke Weltatlas (Burgermeister & Topel 1992). Data concerning the climate of the Kaliningrad region was taken from Orlenok *et al.* (1998). The simplified Mutual Climatic Range (MCR) method was used for palaeoclimate reconstruction based on fossil beetle assemblages. The palaeoclimate was determined on the basis of modern climate of the territories with maximal taxon concentration and the greatest amount of range overlaps. Complications, such as the supraspecific level of taxonomic data used, the incomplete distributional information available, and the unclear altitudinal and climatic information concerning several taxa, yield generalized reconstructions that can be refined with the addition of more data.

Results

A synoptic list of the beetle genera from the middle-upper Eocene European ambers (Baltic amber *s.l.*):

Suborder ARCHOSTEMATA

Family Cupedidae Laporte de Castelnau, 1836

1. *Cupes* Fabricius, 1801 [BaA—7 spp.]; Recent: Afrotropical, Australian, Nearctic, Oriental, Palaearctic (E). Fig.1.
2. *Taxopsis* Kirejtshuk, Nel et Kirejtshuk, 2016 [BaA—1 sp.]; fossil.

Family Micromalthidae Barber, 1913

3. *Micromalthus* LeConte, 1878 [RoA—1 sp.]; Recent: Nearctic (E). Fig.2.

Suborder ADEPHAGA

Family Gyrinidae Latreille, 1810
4. *Gyrinoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.

Family Dytiscidae Leach, 1815
5. *Copelatus* Erichson, 1832 [BaA—1 sp.]; Recent: cosmopolitan (pantropical, in Palaearctic only S).
6. *Derovatellus* Sharp, 1882 [BaA—1 sp.]; Recent: Afrotropical, Neotropical, Oriental. Fig.3.
7. *Hydroporus* Clairville, 1806 [BaA—1 sp.]; Recent: Holarctic, Neotropical.
8. *Hydrotrupes* Sharp, 1882 [BaA—1 sp.]; Recent: Nearctic (W), Palaearctic (E). Fig.4.

Family Carabidae Latreille, 1802
9. *Agatoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
10. *Arthropterites* Wasmann, 1925 [BaA—1 sp.]; fossil.
11. *Bembidion* Latreille, 1802 [BaA—2 spp.]; Recent: cosmopolitan (mostly in temperate areas).
12. *Calathus* Bonelli, 1810 [BaA—1 sp.]; Recent: Afrotropical (montane), Holarctic, Neotropical (N).
13. *Cerapterites* Wasmann, 1925 [BaA—1 sp.]; fossil.
14. *Coptodera* Dejean 1825 [BaA—1 sp.]; Recent: sub-cosmopiltan (non-European). Fig.5.
15. *Cymindoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
16. *Dromius* Bonelli, 1809 [BaA—2 spp.]; Recent: cosmopolitan.
17. *Dyschiriomimus* Iablokoff-Khnzorian, 1960 [BaA—1 sp.]; fossil.
18. *Eopaussus* Wasmann, 1926 [BaA—1 sp.]; fossil.
19. *Elaphropus* Motschulsky, 1839 [BaA—1 sp.]; Recent: cosmopolitan.
20. *Limodromus* Motschulsky, 1850 [BaA—1 sp.]; Recent: Holarctic, Oriental (N).
21. *Loricera* Latreille, 1802 [BaA—2 spp.]; Recent: Holarctic, Oriental (N).
22. *Pleurarthropterus* Wasmann, 1927 [BaA—12 spp.]; fossil.
23. *Protocerapterus* Wasmann, 1926 [BaA—2 spp.]; fossil.
24. *Protoscalidion* Schaufuss, 1888 [BaA—1 sp.]; fossil.
25. *Succinarthropterus* Kolbe, 1926 [BaA—3 spp.]; fossil.
26. *Trechus* Clairville, 1806 [BaA—3 spp.]; Recent: Afrotropical, Holarctic, Oriental.

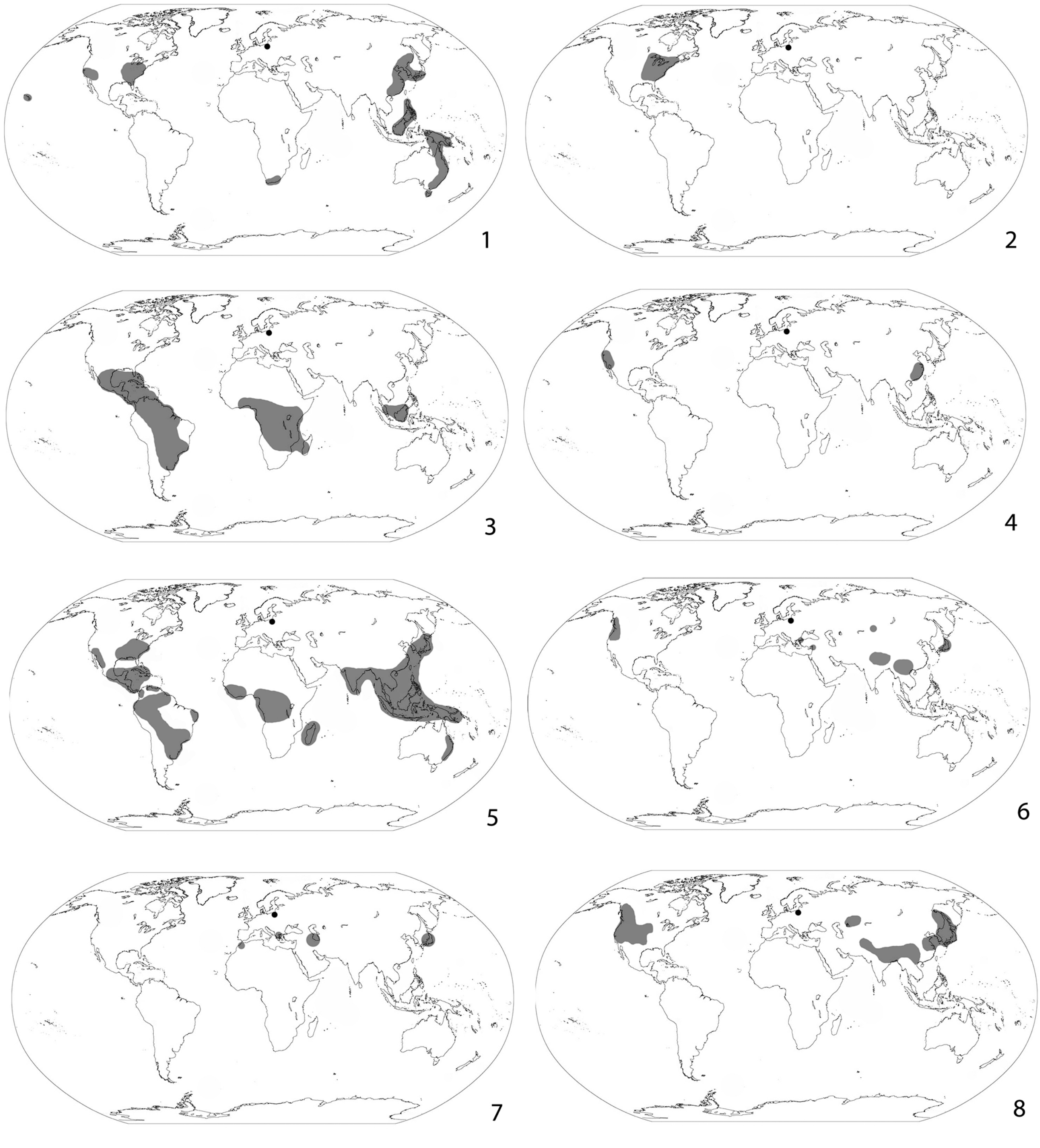
Suborder POLYPHAGA

Family Histeridae Gyllenhal, 1808
27. *Carcinops* Marseul, 1855 [BaA—1 spp.]; Recent: cosmopolitan.
28. *Xestipyge* Marseul, 1862 [BaA—1 sp.]; Recent: Afrotropical, Holarctic, Oriental.

Family Agyrtidae Thomson, 1859
29. *Ipelates* Reitter, 1884 [BaA—1 sp.; BiA—1 sp.]; Recent: Nearctic (W), Oriental (N), Palaearctic. Fig.6.

Family Leiodidae Fleming, 1821
30. *Catops* Paykull, 1798 [BaA—2 spp.]; Recent: Holarctic, Oriental (N).
31. *Nemadus* C.G. Thomson, 1867 [BaA—1 sp.]; Recent: Holarctic.
32. *Prionochaeta* Horn, 1880 [RoA—1 sp.]; Recent: Holarctic (non-European).
33. *Tafforeus* Perreau, 2012 [BaA—1 sp.]; fossil.

Family Ptiliidae Erichson, 1845
34. *Micridium* Flach, 1888 [BaA—1 sp.]; Recent: Holarctic.
35. *Microptilium* Matthews, 1872 [BaA—1 sp.]; Recent: Palaearctic.
36. *Ptinella* Flach, 1888 [BaA—1; RoA—1 sp.]; Recent: cosmopolitan.



FIGURES 1–8. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **1)** *Cupes*; **2)** *Micromalthus*; **3)** *Derovatellus*; **4)** *Hydrotrupes*; **5)** *Coptodera*; **6)** *Ipelates*; **7)** *Dictyon*; **8)** *Heterlimnius*.

Family Staphylinidae Latreille, 1802

37. *Adinopsis* Cameron, 1919 [BaA—1 sp.]; Recent: Afrotropical, Australian, Nearctic, Neotropical, Oriental.
38. *Aenictosoma* Schaufuss, 1891 [BaA—1 sp.]; fossil.
39. *Aleochara* Gravenhorst, 1802 [BaA—1 sp.]; Recent: cosmopolitan.
40. *Atheta* Thomson, 1910 [BaA—1 sp.]; Recent: cosmopolitan.
41. *Baltioligota* Paśnik, 2005 [BaA—1 sp.]; fossil.
42. *Baltostigus* Jałoszyński, 2016 [BaA—2 spp.]; fossil.
43. *Batrisus* Aubé, 1833 [BaA—2 spp.]; Recent: Palaearctic.
44. *Bembicidiodes* Schaufuss, 1889 [BaA—1 sp.]; fossil.

45. *Bolitobius* Samouelle, 1819 [BaA—1 sp.]; Recent: Holarctic.
46. *Bythinus* Leach, 1817 [BaA—4 spp.]; Recent: Palaearctic (W).
47. *Cephennodes* Reitter, 1884 [BaA—0]; Recent: Palaearctic.
48. *Cephennomicrus* Reitter, 1907 [RoA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Oriental, Palaearctic (E).
49. *Chevrolatia* Jacquelin du Val, 1850 [BaA—0]; Recent: Afrotropical, Holarctic.
50. *Cryptodiodon* Schaufuss, 1890 [BaA—1 sp.]; fossil.
51. *Ctenistodes* Schaufuss, 1890 [BaA—1 sp.]; fossil.
52. *Cymbalizion* Schaufuss, 1890 [BaA—1 sp.]; fossil.
53. *Dantiscanus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
54. *Deuterotyrus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
55. *Dictyon* Fauvel, 1900 [BaA—1 sp.]; Recent: Palaearctic (S). Fig.7.
56. *Diochus* Erichson, 1839 [BaA—1 sp.]; Recent: cosmopolitan.
57. *Electrogymnusa* Wolf-Schwenninger, 2004 [BaA—1 sp.]; fossil.
58. *Electroscydmaenus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
59. *Euaesthetus* Gravenhorst, 1806 [BaA—0]; Recent: Nearctic, Neotropical (N), Oriental, Palaearctic.
60. *Euconnus* Thomson, 1859 [BaA—4 spp.; RoA—1 sp.]; Recent: cosmopolitan.
61. *Euplectus* Leach, 1817 [BaA—3 spp.]; Recent: cosmopolitan.
62. *Euroleptochromus* Jałoszyński, 2012 [BaA—1 sp.]; fossil.
63. *Euspinoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
64. *Faronus* Aubé, 1844 [BaA—2 spp.]; Recent: Palaearctic (W).
65. *Glaesoconnus* Jałoszyński et Perkovsky, 2016 [RoA—1 sp.]; fossil.
66. *Greys* Schaufuss, 1890 [BaA—1 sp.]; fossil.
67. *Hagnometopias* Schaufuss, 1890 [BaA—1 sp.]; fossil.
68. *Hetereuplectes* Schaufuss, 1890 [BaA—1 sp.]; fossil.
69. *Hetereuthia* Schaufuss, 1890 [BaA—1 sp.]; fossil.
70. *Heuretus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
71. *Lathrobium* Gravenhorst, 1802 [BaA—5 spp.]; Recent: cosmopolitan.
72. *Leptusa* Kraatz, 1856 [RoA—1 sp.]; Recent: cosmopolitan.
73. *Monyx* Schaufuss, 1890 [BaA—1 sp.]; fossil.
74. *Nugaculus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
75. *Nugator* Schaufuss, 1890 [BaA—1 sp.]; fossil.
76. *Octavius* Fauvel, 1873 [BaA—0]; Recent: Afrotropical, Australian, Neotropical, Madagascar, Palaearctic (W), Oriental.
77. *Oxyporus* Fabricius, 1775 [BaA—1 sp.]; Recent: Holarctic.
78. *Palaeomastigus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
79. *Palaeomesoporus* Yamamoto et Maruyama, 2017 [BaA—1 sp.]; fossil.
80. *Palaeosepidophilus* Paśnik et Kubisz, 2002 [BaA—1 sp.]; fossil.
81. *Palaeothia* Schaufuss, 1890 [BaA—1 sp.]; fossil.
82. *Pammiges* Schaufuss, 1890 [BaA—1 sp.]; fossil.
83. *Pantobatrisus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
84. *Parabryaxis* Schaufuss, 1890 [BaA—1 sp.]; fossil.
85. *Paraphloeostiba* Steel, 1960 [BaA—1 sp.]; Recent: Afrotropical, Australian, Oriental, Palaearctic (SE).
86. *Phyllodrepa* Thomson, 1859 [BaA—1 sp.]; Recent: Holarctic, Oriental (N).
87. *Phymatura* J. Sahlberg, 1876 [BaA—1 sp.]; Recent: Holarctic.
88. *Pseudolesteva* Schaufuss, 1890 [BaA—1 sp.]; fossil.
89. *Rovnoleptochromus* Jałoszyński et Perkovsky, 2016 [RoA—1 sp.]; fossil.
90. *Rovnoscydmus* Jałoszyński et Perkovsky, 2016 [RoA—2 spp.]; fossil.
91. *Rybaxis* Saulsy, 1876 [BaA—3 spp.]; Recent: Afrotropical, Australian, Holarctic, Oriental.
92. *Scydmaenoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
93. *Semnodiocerus* Schaufuss, 1890 [BaA—1 sp.]; fossil.
94. *Sepedophilus* Gistel, 1856 [BaA—1 sp.]; Recent: cosmopolitan.

95. *Stenaesthetus* Sharp, 1874 [BaA—0]; Recent: Afrotropical, Madagascar, Oriental, Palaearctic (E).
96. *Stenichnus* Thomson, 1862 [BaA—4 spp.; RoA—1 sp.]; Recent: cosmopolitan.
97. *Stenus* Latreille, 1796 [BaA—9 spp.]; Recent: cosmopolitan.
98. *Tachyporus* Gravenhorst, 1802 [BaA—1 sp.]; Recent: Afrotropical, Australian, Holarctic, Oriental.
99. *Tmesiphoroides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
100. *Tychus* Leach, 1817 [BaA—2 spp.]; Recent: Palaearctic.
101. *Tyrus* Aubé, 1833 [BaA—1 sp.]; Recent: Holarctic, Oriental.
102. *Vertheia* Jałoszyński et Perkovsky, 2016 [RoA—1 sp.]; fossil.

Family Lucanidae Latreille, 1804
103. *Dorcasoides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
104. *Paleognathus* Waga, 1883 [BaA—1 sp.]; fossil.
105. *Succiniplatycerus* Nikolajev, 1990 [BaA—1 sp.]; fossil.

Family Scarabaeidae Latreille, 1802
106. *Ataenius* Harold, 1867 [BaA—1 sp.]; Recent: cosmopolitan.
107. *Saprosites* Redtenbacher, 1857 [BaA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Neotropical, Oriental.

Family Scirtidae Fleming, 1821
108. *Brachelodes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
109. *Cyphon* Paykull, 1799 [BaA—9 spp.]; Recent: Holarctic, Neotropical, Oriental.
110. *Cyphonogenius* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
111. *Elodes* Latreille, 1796 [BaA—7 spp.]; Recent: Holarctic, Oriental.
112. *Microcara* Thomson, 1859 [BaA—4 spp.]; Recent: Holarctic, Oriental.
113. *Plagiocyphon* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.

Family Elmidae Curtis, 1830
114. *Heterlimnius* Hinton 1935 [BaA—1 sp.]; Recent: Nearctic, Oriental (N), Palaearctic (E). Fig.8.
115. *Heterelmis* Sharp 1882 [BaA—1 sp.]; Recent: Nearctic (S), Neotropical. Fig.9.

Family Limnichidae Erichson, 1846
116. *Palaeoersachus* Pütz, Hernando et Ribera, 2004 [BaA—1 sp.]; fossil.

Family Ptilodactylidae Laporte de Castelnau, 1836
117. *Electrolichas* Alekseev et Jäch, 2016 [BaA—1 sp.]; fossil.
118. *Ptilodactyloides* Motschulsky, 1856 [BaA—1 sp.]; fossil.

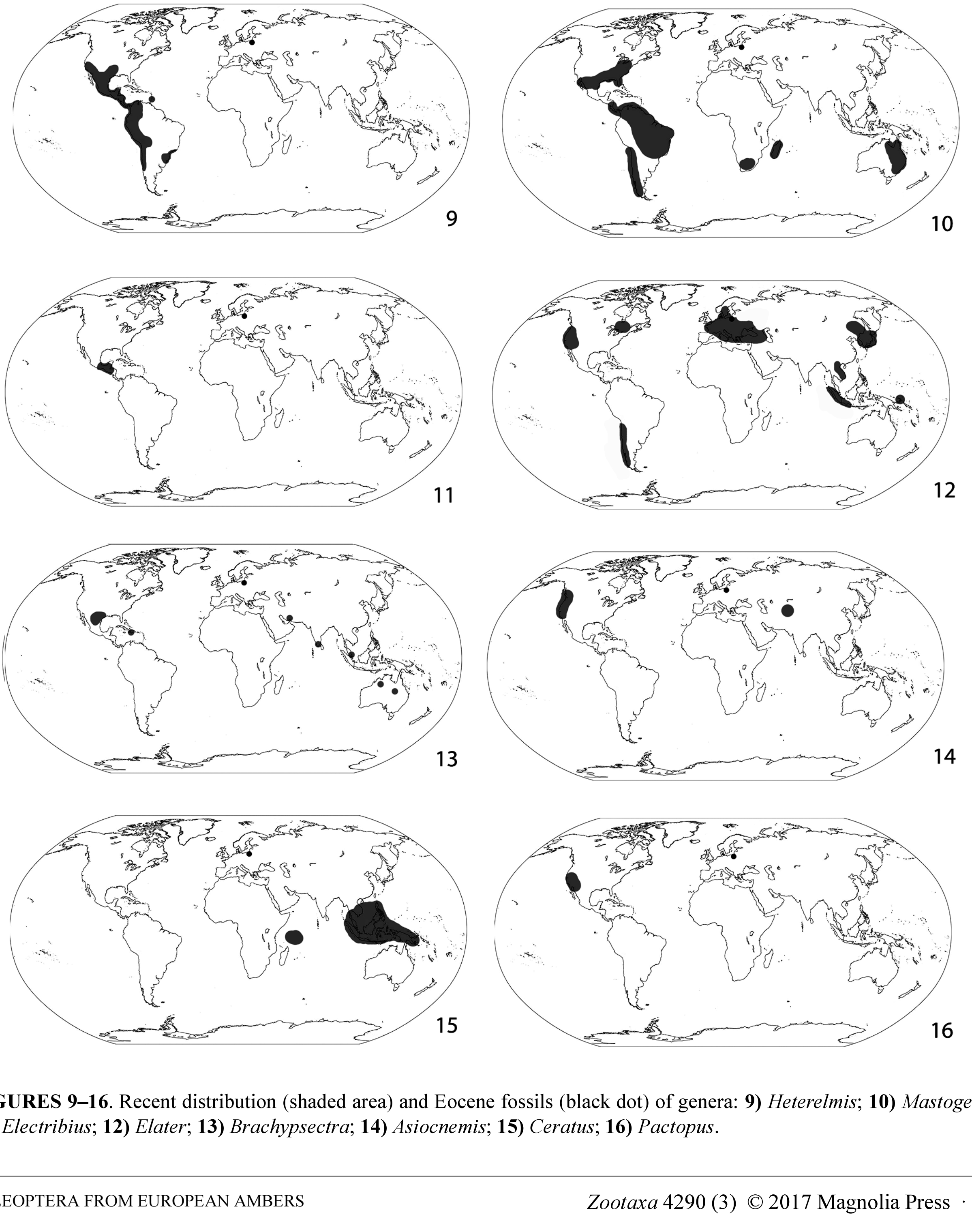
Family Buprestidae Leach, 1815
119. *Mastogenius* Solier, 1849 [BaA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Nearctic, Neotropical. Fig.10.

Family Schizopodidae LeConte, 1859
120. *Electrapate* Iablokoff-Khnzorian, 1962 [BaA—1 sp.]; fossil.

Family Artematopodidae Lacordaire, 1857
121. *Electribius* Crowson, 1973 [BaA—5 spp.]; Recent: Neotropical (N). Fig.11.
122. *Protartematopus* Crowson, 1973 [BaA—1 sp.]; fossil.

Family Elateridae Leach, 1815
123. *Abelater* Fleutiaux, 1947 [BaA—1 sp.]; Recent: Oriental, Palaearctic (E).
124. *Athous* Eschscholtz, 1829 [BaA—1 sp.]; Recent: Holarctic, Oriental.

125. *Cardiophorus* Eschscholtz, 1829 [BaA—1 sp.]; Recent: cosmopolitan.
126. *Crioraphes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
127. *Diaraphes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
128. *Elater* Linnaeus, 1758 [BaA—1 sp.]; Recent: Holarctic, Neotropical, Oriental. Fig.12.
129. *Elatron* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
130. *Holopleurus* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
131. *Limonius* Eschscholtz, 1829 [BaA—1 sp.]; Recent: Holarctic.
132. *Megapenthes* Kiesenwetter, 1858 [BaA—3 spp.]; Recent: cosmopolitan.
133. *Orthoraphes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
134. *Plagioraphes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
135. *Tetraraphes* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.



FIGURES 9–16. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **9)** *Heterelmis*; **10)** *Mastogenius*; **11)** *Electribius*; **12)** *Elater*; **13)** *Brachypsectra*; **14)** *Asiocnemis*; **15)** *Ceratus*; **16)** *Pactopus*.

Family Brachypsectridae LeConte and Horn, 1883

136. *Brachypsectra* LeConte et Horn, 1883 [BaA—0]; Recent: Australian, Nearctic, Neotropical (N), Oriental. Fig.13.

Family Eucnemidae Eschscholtz, 1829

137. *Arisus* Bonvouloir, 1871 [BaA—0]; Recent: Australian, Oriental.
138. *Asiocnemis* Mamaev, 1976 [BaA—0]; Recent: Nearctic (W), Palaearctic (non-European). Fig.14.
139. *Balistica* Motschulsky, 1861 [BaA—1 sp.]; Recent: Oriental.
140. *Ceratus* Bonvouloir, 1871 [BaA—1 sp.]; Recent: Afrotropical, Oriental. Fig.15.
141. *Discharachthis* Blackburn, 1900 [BaA—2 spp.]; Recent: Australian, Neotropical, Oriental, Palaearctic (E).
142. *Dromeolus* Kiesenwetter, 1858 [BaA—0]; Recent: cosmopolitan.
143. *Erdaia* Muona, 1993 [BaA—2 spp.]; fossil.
144. *Euryptychus* LeConte, 1852 [BaA—2 spp.]; Recent: cosmopolitan.
145. *Fornax* Laporte de Castelnau, 1835 [BaA—0]; Recent: cosmopolitan (non-European).
146. *Hemiopsida* MacLeay, 1872 [BaA—0]; Recent: Australian, Nearctic, Oriental.
147. *Hylis* Des Gozis, 1886 [BaA—1 sp.]; Recent: Holarctic.
148. *Microrhagus* Dejean, 1833 [BaA—0]; Recent: cosmopolitan.
149. *Poecilochrus* Bonvouloir, 1871 [BaA—0]; Recent: cosmopolitan (non-European).
150. *Rhagomicrus* Fleutiaux, 1902 [BaA—0]; Recent: Afrotropical, Neotropical, Palaearctic, Oriental.
151. *Sieglindea* Muona, 1993 [BaA—2 spp.]; fossil.
152. *Spinifornax* Fleutiaux, 1926 [BaA—1 sp.]; Recent: Australian, Neotropical, Palaearctic (E).
153. *Throscogenius* Iablokoff-Khnzorian, 1962 [BaA—1 sp.]; fossil.

Family Throscidae Laporte de Castelnau, 1840

154. *Aulonothroscus* Horn, 1890 [BaA—1 sp.]; Recent: cosmopolitan.
155. *Jaira* Muona, 1993 [BaA—1 sp.]; fossil.
156. *Pactopus* LeConte, 1852 [BaA—2 spp.]; Recent: Nearctic (W). Fig.16.
157. *Potergus* Fleutiaux, 1926 [BaA—2 spp.]; Recent: Australian, Oriental.
158. *Trixagus* Kugelann, 1794 [BaA—1 sp.]; Recent: cosmopolitan.

Family Berendtimiridae Winkler, 1987

159. *Berendtimirus* Winkler, 1987 [BaA—1 sp.]; fossil.

Family Omalisidae Lacordaire, 1857

160. *Jantarokrama* Kirejtshuk et Kovalev, 2015 [BaA—1 sp.]; fossil.

Family Lycidae Laporte de Castelnau, 1840

161. *Helcophorus* Fairmaire, 1891 [BaA—1 sp.]; Recent: Oriental (N), Palaearctic (E). Fig.17.
162. *Kolibacium* Winkler, 1987 [BaA—1 sp.]; Recent: Oriental (N), Palaearctic (E). Fig.18.
163. *Protolopheros* Kazantsev, 2013 [BaA—1 sp.]; fossil.
164. *Pseudoplatopterus* Kleine, 1940 [BaA—1 sp.]; Recent: Nearctic (E), Oriental (N), Palaearctic (E). Fig.19.

Family Lampyridae Rafinesque, 1815

165. *Electrotreta* Kazantsev, 2012 [BaA—1 sp.]; fossil.
166. *Eoluciola* Kazantsev, 2013 [BaA—1 sp.]; fossil.

Family Omethidae LeConte, 1861

167. *Electromethes* Kazantsev, 2012 [BaA—1 sp.]; fossil.

Family Cantharidae Latreille, 1802

168. *Cantharis* Linnaeus, 1758 [BaA—2 spp.]; Recent: Holarctic.
169. *Cacomorphocerus* Schaufuss, 1891 [BaA—2 spp.]; fossil.

170. *Curche* Alekseev et Kazantsev, 2014 [BaA—1 sp.]; fossil.
171. *Electronycha* Kazantsev, 2013 [BaA—1 sp.]; fossil.
172. *Electrosilis* Kazantsev, 2013 [BaA—1 sp.]; fossil.
173. *Macrocerus* Motschulsky 1845 [BaA—1 sp.]; Recent: Palaearctic (E).
174. *Malthinus* Latreille, 1806 [BaA—1 sp.]; Recent: Holarctic, Neotropical (N), Oriental.
175. *Malthodes* Kiesenwetter, 1852 [BaA—4 spp.; RoA—2 spp.]; Recent: Afrotropical, Holarctic, Neotropical, Oriental.
176. *Mimoplatycis* Kazantsev, 2013 [BaA—1 sp.]; fossil.
177. *Rhagonycha* Eschscholtz, 1830 [BaA—2 spp.]; Recent: Holarctic.
178. *Sucinocantharis* Kuśka et Kania, 2010 [BaA—1 sp.]; fossil.
179. *Sucinorhagonycha* Kuska, 1996 [BaA—1 sp.]; fossil.
180. *Themus* Motschulsky, 1858 [BaA—1 sp.]; Recent: Oriental, Palaearctic (E).

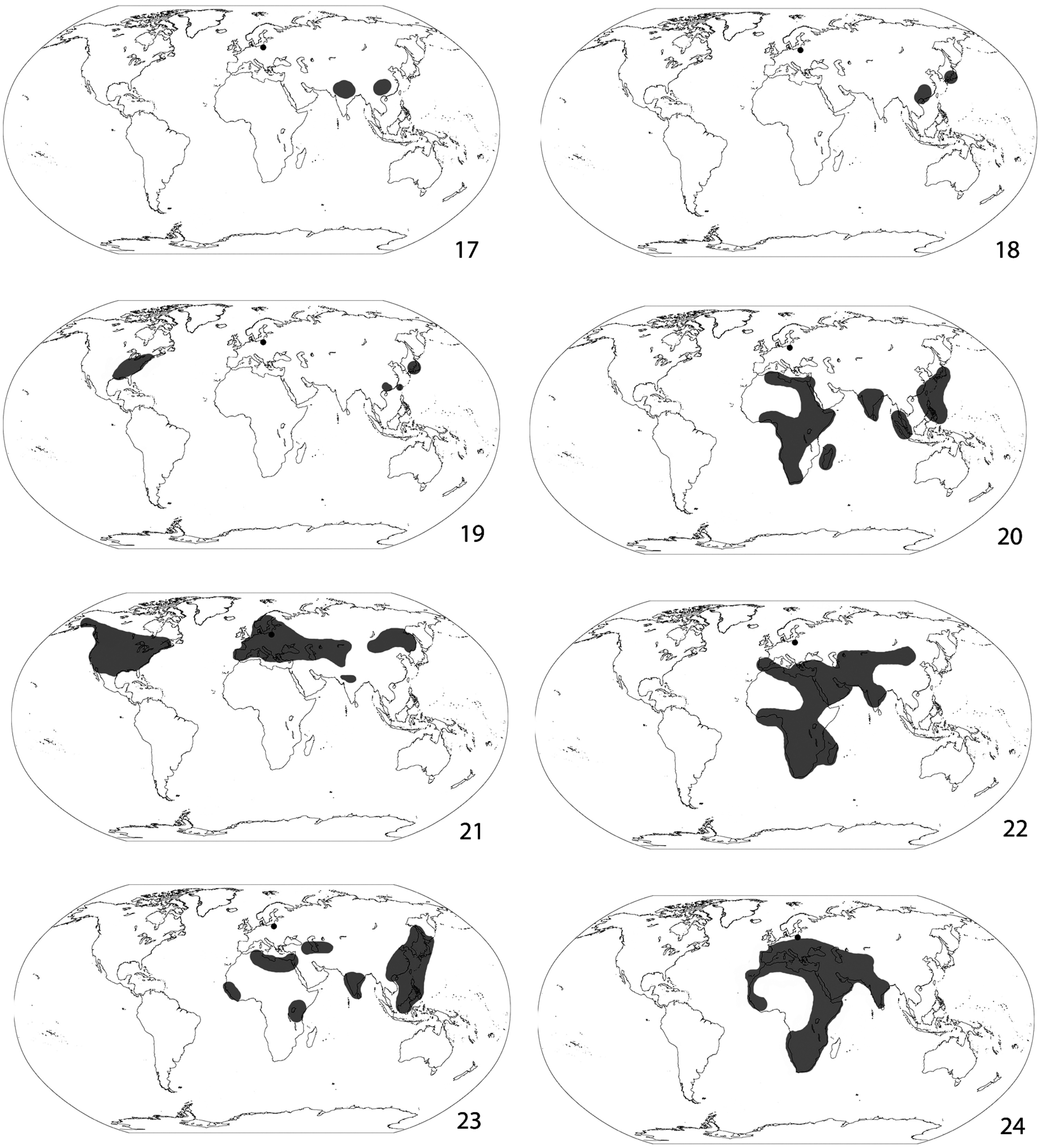
Family Jacobsoniidae Heller, 1926
181. *Derolathrus* Sharp, 1908 [BaA—1 sp.]; Recent: cosmopolitan.

Family Dermestidae Latreille, 1807
182. *Anthrenus* Schaeffer, 1766 [BaA—4 spp.]; Recent: cosmopolitan.
183. *Attagenus* Latreille, 1802 [BaA—6 spp.]; Recent: Afrotropical, Australian, Holarctic, Oriental.
184. *Dermestes* Linnaeus, 1758 [BaA—1 sp.; RoA—1 sp.]; Recent: cosmopolitan.
185. *Evorinea* Beal, 1961 [BaA—1 sp.]; Recent: Afrotropical, Madagascar, Oriental, Palaearctic (S). Fig.20.
186. *Globicornis* Latreille, 1829 [BaA—3 spp.]; Recent: Holarctic.
187. *Megatoma* Herbst, 1792 [BaA—1 sp.]; Recent: Holarctic. Fig.21.
188. *Phradonoma* Jacquelin du Val, 1859 [BaA—1 sp.]; Recent: Afrotropical, Palaearctic. Fig.22.
189. *Trinodes* Dejean, 1821 [BaA—1 sp.]; Recent: Palaearctic, Afrotropical, Oriental. Fig.23.
190. *Trogoderma* Dejean, 1821 [BaA—1 sp.]; Recent: cosmopolitan.

Family Bostrichidae Latreille, 1802
191. *Stephanopachys* Waterhouse, 1888 [BaA—2 spp.]; Recent: Holarctic.

Family Ptinidae Latreille, 1802
192. *Dignomus* Wollaston, 1862 [BaA—1 sp.]; Recent: Afrotropical, Oriental, Palaearctic. Fig.24.
193. *Dryophilus* Chevrolat, 1832 [BaA—1 sp.]; Recent: Palaearctic (W). Fig.25.
194. *Episernus* Thomson, 1863 [BaA—1 sp.]; Recent: Holarctic.
195. *Ernobius* Thomson, 1859 [BaA—5 spp.]; Recent: Holarctic.
196. *Eucrada* LeConte, 1861 [BaA—1 sp.]; Recent: Nearctic. Fig.26.
197. *Gastrallus* Jacquelin du Val, 1860 [BaA—1 sp.]; Recent: Afrotropical, Australian (N), Holarctic, Madagascar, Oriental. Fig.27.
198. *Hadrobregmus* Thomson, 1859 [BaA—1 sp.]; Recent: Palaearctic.
199. *Hemicoelus* LeConte, 1861 [BaA—1 sp.]; Recent: Holarctic.
200. *Homophthalmus* Abeille, 1875 [BaA—1 sp.]; Recent: Afrotropical (S), Palaearctic (W). Fig.28.
201. *Microbregma* Seidlitz, 1889 [BaA—2 spp.]; Recent: Holarctic. Fig.29.
202. *Petalium* LeConte, 1861 [BaA—0]; Recent: Afrotropical, Nearctic, Neotropical, Madagascar.
203. *Ptinus* Linnaeus, 1767 [BaA—4 spp.]; Recent: cosmopolitan.
204. *Sucinoptinus* Belles et Vitali, 2007 [BaA—2 spp.; RoA—2 spp.]; fossil.
205. *Trichodesma* LeConte, 1861 [BaA—0]; Recent: Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic (E).
206. *Tuberernobius* Zahradník et Háva, 2014 [BaA—1 sp.]; fossil.
207. *Xylasia* Zahradník et Háva, 2014 [BaA—1 sp.]; fossil.

Family Biphyllidae Sharp, 1900 (1861)
208. *Diplocoelus* Guérin-Méneville, 1844 [BaA—1 sp.]; Recent: Australian, Holarctic, Neotropical, Oriental. Fig.30.



FIGURES 17–24. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **17)** *Helcophorus*; **18)** *Kolibacium*; **19)** *Pseudoplatopterus*; **20)** *Evorinea*; **21)** *Megatoma*; **22)** *Phradonoma*; **23)** *Trinodes*; **24)** *Dignomus*.

Family Lymexylidae Fleming, 1821

209. *Ponomarenkylon* Kirejtshuk, 2008 [BaA—1 sp.]; fossil.

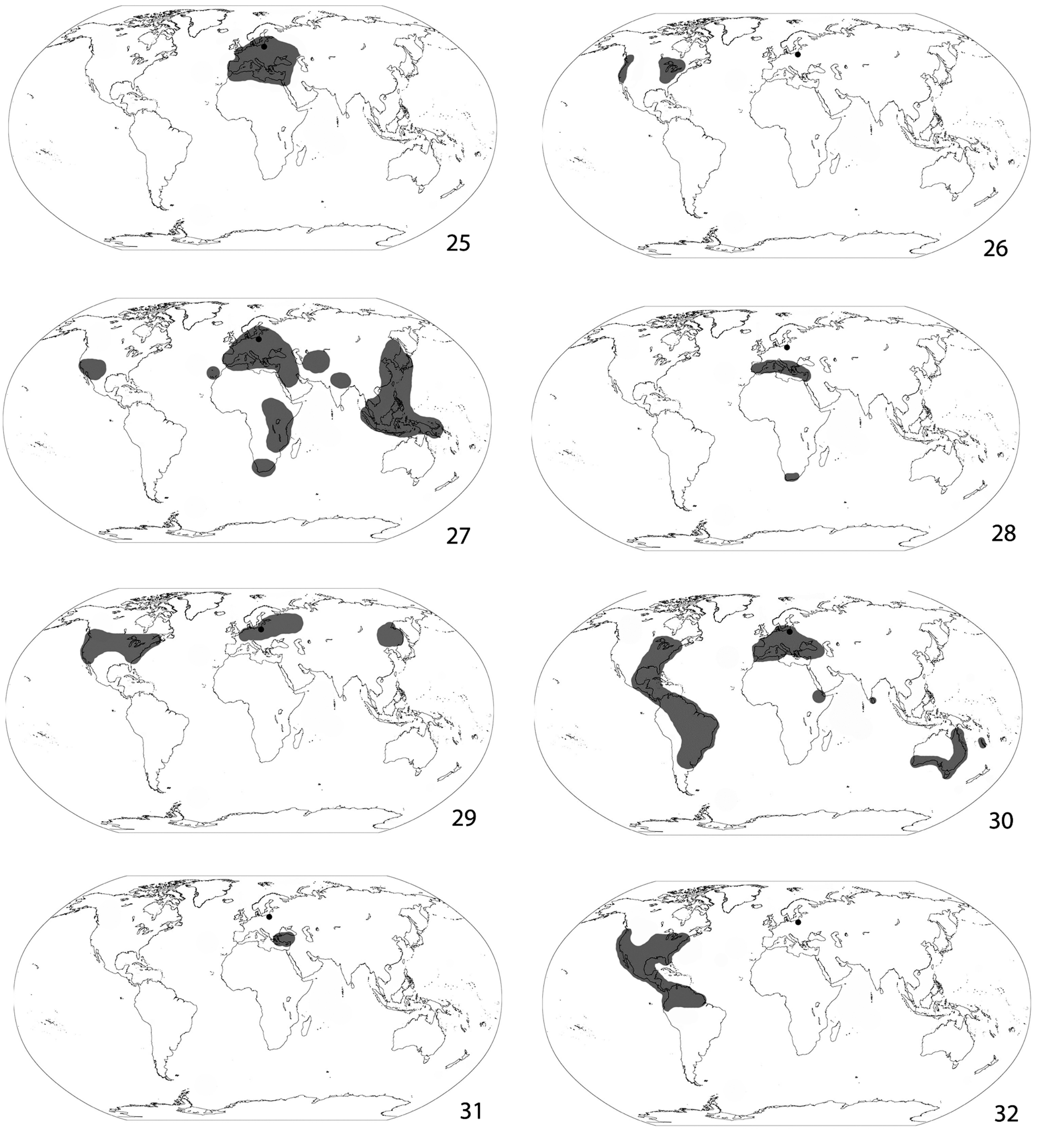
Family Trogossitidae Latreille, 1802

210. *Promanodes* Kolibac, Schmied, Wappler, Kubisz, 2010 [BaA—2 spp.]; fossil.
211. *Seidlitzella* Jakobson, 1915 [BaA—0]; Recent: Palaearctic (W). Fig.31.

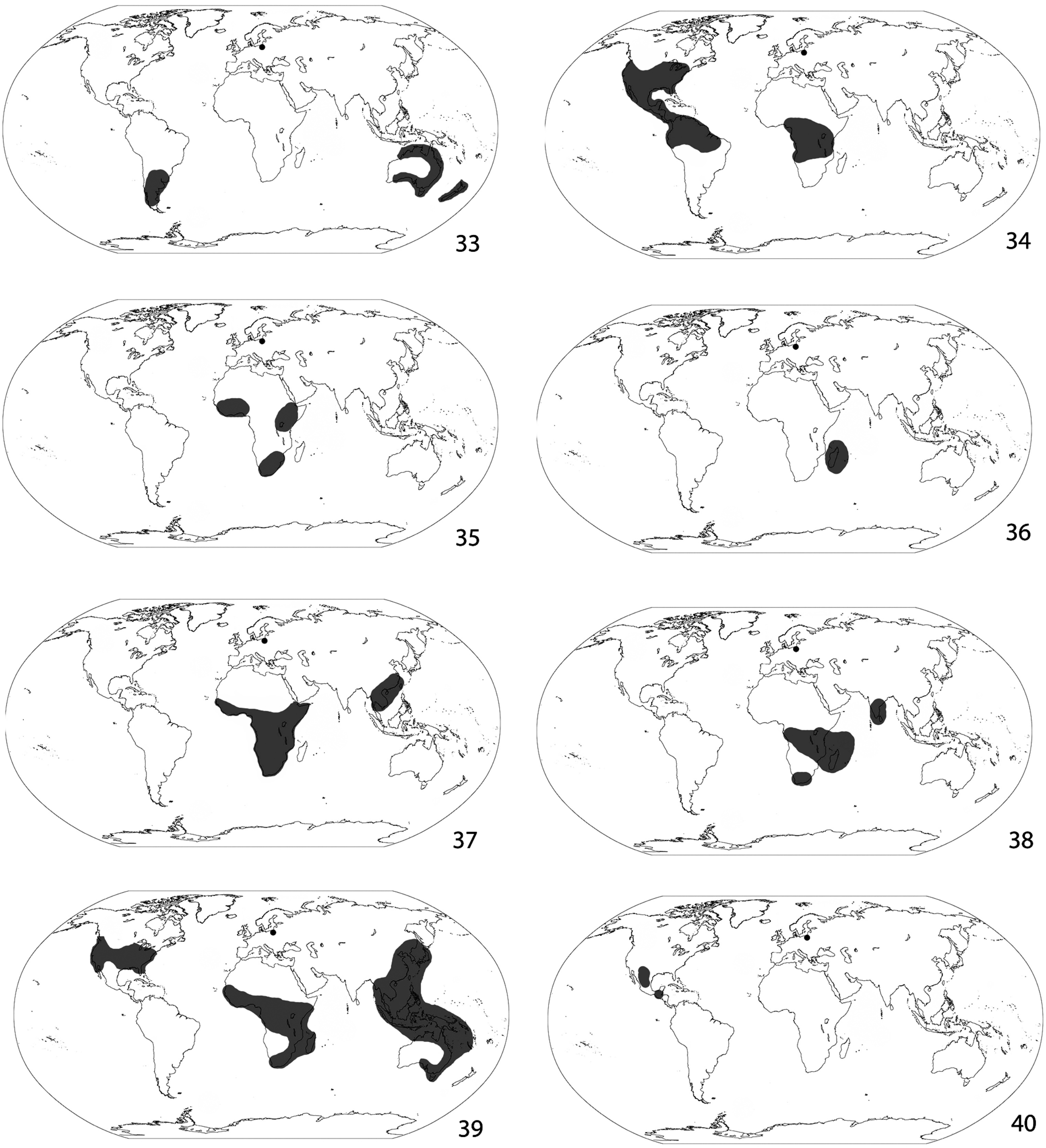
Family Cleridae Latreille, 1802

212. *Aberrocorynetes* Winkler, 1990 [BaA—1 sp.]; fossil.
213. *Bilbotillus* Kolibac, 1997 [BaA—1 sp.]; fossil.
214. *Cymatodera* Grey, 1832 [BaA—2 spp.]; Recent: Nearctic, Neotropical. Fig.32.

215. *Lemidia* Spinola, 1841 [BaA—1 sp.]; Recent: Australian, Neotropical. Fig.33.
216. *Mitrandiria* Kolibac, 1997 [BaA—1 sp.]; fossil.
217. *Orthrius* Gorham, 1876 [BaA—2 spp.]; Recent: Oriental, Palaearctic (E).
218. *Phyllobaenus* Dejean, 1837 [BaA—1 sp.]; Recent: Afrotropical, Nearctic, Neotropical. Fig.34.
219. *Prosymnus* Laporte de Castelnau, 1836 [BaA—1 sp.]; Recent: Afrotropical. Fig.35.
220. *Pseudopallenis* Kuwert, 1893 [BaA—3 spp.]; Recent: Madagascar. Fig.36.
221. *Smudlotillus* Kolibac, 1997 [BaA—1 sp.]; fossil.
222. *Strotocera* Schenkling, 1902 [BaA—1 sp.]; Recent: Afrotropical, Orienal, Palaearctic (E). Fig.37.
223. *Thanasimoides* Murray, 1867 [BaA—1 sp.]; Recent: Afrotropical.
224. *Zahradnikius* Winkler, 1992 [BaA—1 sp.]; fossil.



FIGURES 25–32. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **25)** *Dryophilus*; **26)** *Eucrada*; **27)** *Gastrallus*; **28)** *Homophthalmus*; **29)** *Microbregma*; **30)** *Diplocoelus*; **31)** *Seidlitzella*; **32)** *Cymatodera*.



FIGURES 33–40. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **33)** *Lemidia*; **34)** *Phyllobaenus*; **35)** *Prosymnus*; **36)** *Pseudopallenis*; **37)** *Strotocera*; **38)** *Xamerpus*; **39)** *Phenolia*; **40)** *Aneurops*.

Family Dasytidae Laporte de Castelnau, 1840
225. *Aploceble* Majer, 1998 [BaA—4 spp.]; fossil.
226. *Aplocnemus* Stephens, 1830 [BaA—0]; Recent: Afrotropical, Oriental, Palaearctic.
227. *Xamerpus* Fairmaire 1886 [BaA—0]; Recent: Afrotropical, Madagascar, Oriental. Fig.38.

Family Malachiidae Fleming, 1821
228. *Colotes* Erichson 1840 [BaA—1 sp.]; Recent: Afrotropical, Palaearctic.
229. *Palpattalus* Tshernyshev, 2016 [BaA—2 spp.]; fossil.
230. *Protocephaloncus* Tshernyshev, 2016 [RoA—1 sp.]; fossil.

Family Cybocephalidae Jacquelin du Val, 1858
231. *Cybocephalus* Erichson, 1844 [BaA—3 spp.]; Recent: Afrotropical, Australia, Holarctic, Oriental.

Family Nitidulidae Latreille, 1802
232. *Baltoraea* Kurochkin et Kirejtschuk, 2010 [BaA—2 spp.]; fossil.
233. *Melipriopsis* Kirejtshuk, 2011 [BaA—1 sp.]; fossil.
234. *Microsoronia* Kirejtshuk et Kurochkin, 2010 [BaA—3 spp.; BiA—1 sp.]; fossil.
235. *Omositoidea* Schaufuss, 1891 [BaA—2 spp.]; fossil.
236. *Phenolia* Erichson, 1843 [BaA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Nearctic, Palaearctic (E). Fig.39.

Family Monotomidae Laporte de Castelnau, 1840
237. *Aneurops* Sharp, 1900 [BaA—1 sp.]; Recent: Nearctic (S), Neotropical (N). Fig.40.
238. *Europs* Wollaston, 1854 [BaA—1 sp.]; Recent: Afrotropical, Madagascar, Nearctic, Neotropical, Oriental, Palaearctic (S).

Family Silvanidae Kirby, 1837
239. *Dendrobrontes* Kireytshuk, 2011 [BaA—1 sp.]; fossil.
240. *Mistran* Alekseev et Bukejs, 2016 [BaA—1 sp.]; fossil.

Family Passandridae Erichson, 1845
241. *Passandra* Dalman in Schoenherr, 1817 [BaA—1 sp.]; Recent: Afrotropical, Madagascar, Neotropical, Oriental. Fig.41.

Family Smicripidae Horn, 1880
242. *Smicrips* LeConte, 1878 [BaA—1 sp.]; Recent: Nearctic (S), Neotropical (N). Fig.42.

Family Phalacridae Leach, 1815
243. *Neolitochropus* Lyubarsky et Perkovsky 2016 [BiA—1 sp.]; fossil.
244. *Stilbus* Seidlitz, 1872 [RoA—1 sp.]; Recent: cosmopolitan.

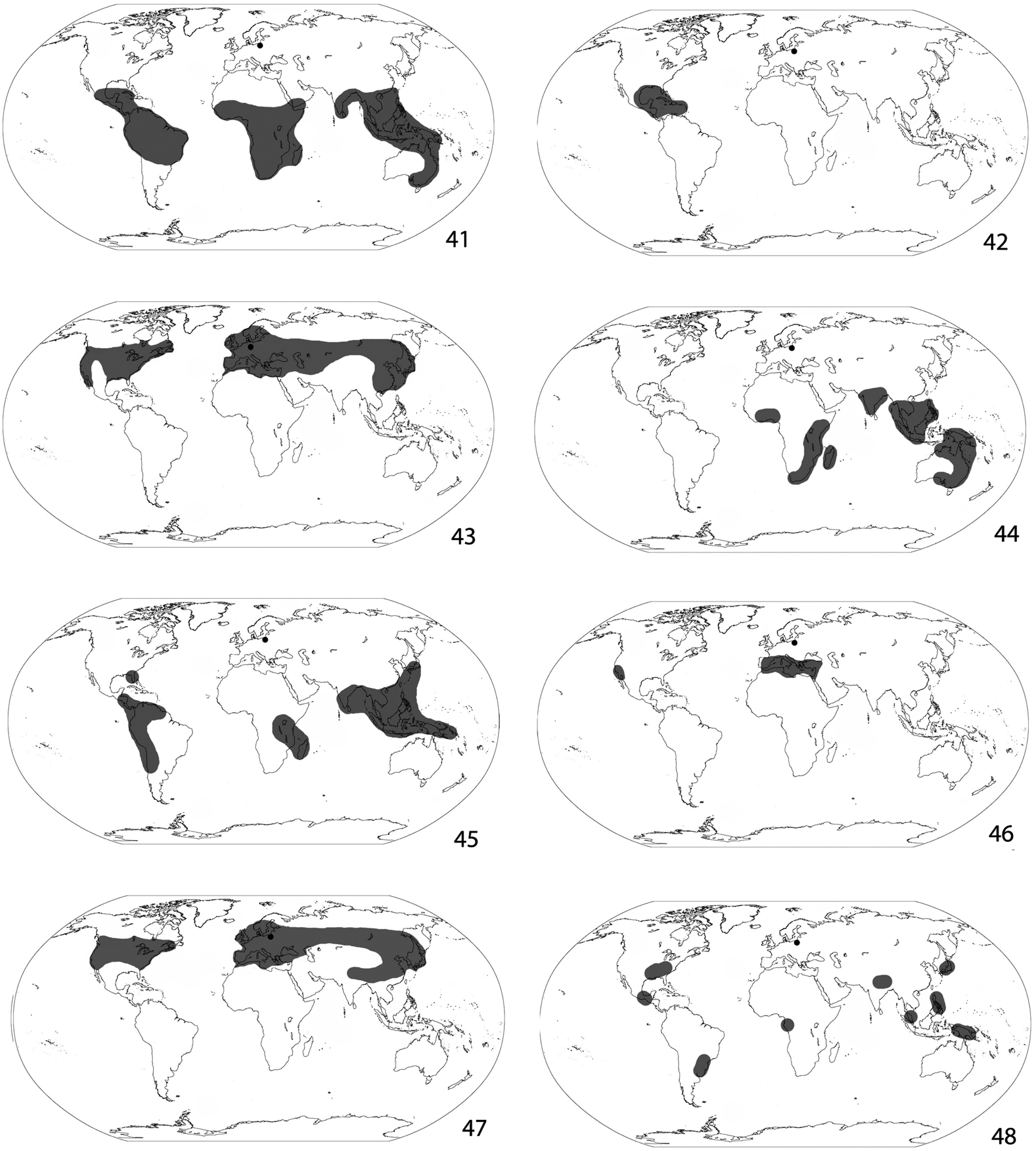
Family Cryptophagidae Kirby, 1837
245. *Atomaria* Stephens, 1830 [BaA—2 spp.]; Recent: cosmopolitan.
246. *Cryptophagus* Herbst, 1863 [RoA—2 spp.]; Recent: cosmopolitan.
247. *Micrambe* Thomson, 1863 [RoA—1 sp.]; Recent: cosmopolitan.

Family Erotylidae Latreille, 1802
248. *Triplax* Herbst, 1793 [BiA—1 sp.]; Recent: Holarctic. Fig.43.
249. *Xenochimatium* Lyubarsky et Perkovsky, 2012 [RoA—1 sp.]; fossil.
250. *Warnis* Lyubarsky, Perkovsky et Alekseev, 2016 [BaA—1 sp.]; fossil.

Family Bothrideridae Erichson, 1845
251. *Pseudobothrideres* Grouvelle, 1908 [BaA—2 spp.]; Recent: Afrotropical, Australian, Madagascar, Oriental. Fig.44.

Family Anamorphidae Strohecker, 1953
252. *Symbiotes* L. Redtenbacher, 1849 [BaA—0]; Recent: Holarctic.

Family Endomychidae Leach, 1815
253. *Holoparamecus* Curtis, 1833 [BaA—0]; Recent: cosmopolitan.
254. *Glesirhanis* Shockley et Alekseev, 2014 [BaA—1 sp.]; fossil.
255. *Phymaphoroides* Motschulsky, 1856 [BaA—1 sp.]; fossil.
256. *Trochoideus* Westwood, 1833 [BaA—0]; Recent: cosmopolitan (non-European). Fig.45.



FIGURES 41–48. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **41)** *Passandra*; **42)** *Smicrips*; **43)** *Triplax*; **44)** *Pseudobothrideres*; **45)** *Trochoideus*; **46)** *Revelieria*; **47)** *Tetratoma*; **48)** *Microscapha*.

Family Corylophidae LeConte, 1852
257. *Clypastraea* Haldeman, 1842 [BaA—1 sp.]; Recent: cosmopolitan.

Family Latridiidae Erichson, 1842
258. *Cartodere* C.G. Thomson, 1859 [BaA—1 sp.]; Recent: cosmopolitan.
259. *Corticaria* Marsham, 1802 [BaA—1 sp.]; Recent: cosmopolitan.
260. *Corticarina* Reitter, 1881 [BaA—2 spp.]; Recent: cosmopolitan.
261. *Dienerella* Reitter, 1911 [BaA—1 sp.]; Recent: cosmopolitan.

262. *Dieneremia* Reike, Alekseev, Bukejs, 2013 [BaA—1 sp.]; fossil.
263. *Enicmis* C.G. Thomson, 1859 [BaA—3 spp.]; Recent: cosmopolitan.
264. *Latridius* Beck, 1812 [BaA—2 spp.]; Recent: cosmopolitan.
265. *Melanophtalma* Motschulsky, 1866 [BaA—2 spp.]; Recent: Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic.
266. *Revelieria* Perris, 1869 [BaA—1 sp.]; Recent: Nearctic (W), Palaearctic (W). Fig.46.
267. *Stephostethus* LeConte, 1878 [BaA—2 spp.]; Recent: Holarctic, Oriental.

Family Mycetophagidae Leach, 1815
268. *Crowsonium* Abdullah, 1964 [BaA—1 sp.]; fossil.

Family Tetratomidae Billberg, 1820
269. *Tetratoma* Fabricius, 1790 [BaA—1 sp.]; Recent: Holarctic. Fig.47.

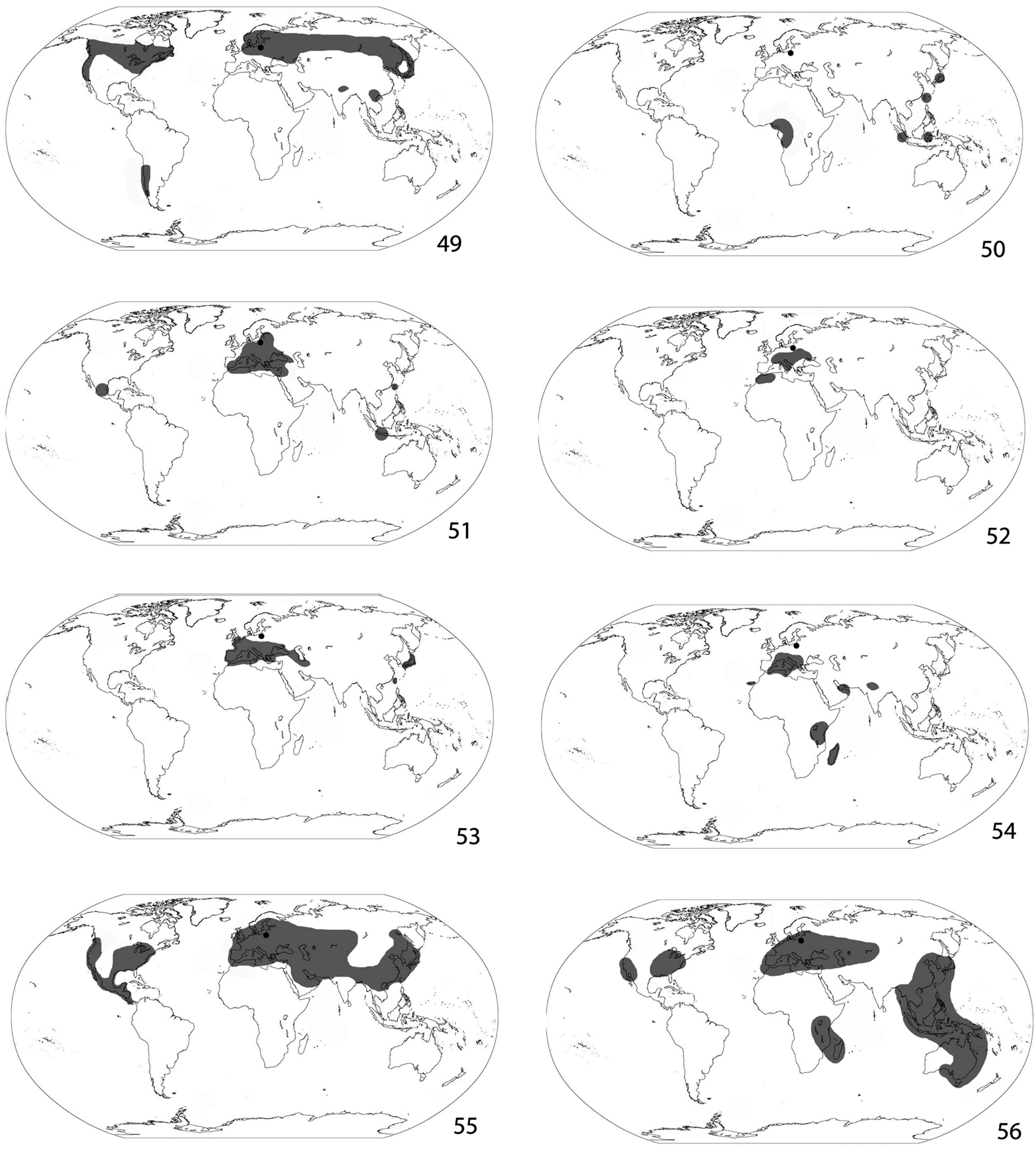
Family Melandryidae Leach, 1815
270. *Abdera* Stephens, 1832 [BaA—2 spp.]; Recent: Holarctic.
271. *Abderina* Seidlitz, 1898 [BaA—1 sp.]; fossil.
272. *Electroabdera* Alekseev, 2014 [BaA—1 sp.]; fossil.
273. *Microscapha* LeConte, 1866 [BaA—1 sp.]; Recent: Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic (E). Fig.48.
274. *Orchesia* Latreille, 1807 [BaA—2 spp.; RoA—1 sp.]; Recent: cosmopolitan.
275. *Quasianisoxya* Alekseev, 2015 [BaA—1 sp.]; fossil.
276. *Serropalpus* Hellenius, 1786 [BaA—3 spp.]; Recent: Holarctic, Neotropic. Fig.49.

Family Mordellidae Latreille, 1802
277. *Glipostena* Ermisch, 1941 [BaA—1 sp.; RoA—1 sp.]; Recent: Afrotropical, Oriental, Palaearctic (E). Fig.50.
278. *Falsomordellistena* Ermisch, 1941 [BaA –1 sp.]; Recent: Madagascar, Neotropical, Oriental, Palaearctic (E).
279. *Mordella* Linnaeus, 1758 [BaA—2 spp.]; Recent: cosmopolitan.
280. *Mordellaria* Ermisch, 1950 [BaA—1 sp.]; Recent: Afrotropical, Madagascar, Neotropic, Oriental, Palaearctic.
281. *Mordellistena* Costa, 1854 [BaA—5 spp.]; Recent: cosmopolitan.
282. *Succimorda* Kubisz, 2001 [BaA—1 sp.]; fossil.

Family Scraptiidae Mulsant, 1856
283. *Anaspis* Geoffroy, 1762 [BaA—4 spp.; RoA—1 sp.]; Recent: cosmopolitan.
284. *Archaeoscraptia* Abdullah, 1964 [BaA—1 sp.]; fossil.
285. *Canifa* Le Conte, 1866 [BaA—0]; Recent: Nearctic, Neotropic (N).
286. *Palaeoscraptia* Abdullah, 1964 [BaA—1 sp.]; fossil.
287. *Scraptia* Latreille, 1807 [BaA—3 spp.]; Recent: cosmopolitan.

Family Ripiphoridae Gemminger, Harold, 1870
288. *Olemehliella* Batelka, 2017 [BaA—1 sp.]; fossil.
289. *Pauroripidius* Kaupp et Nagel, 2001 [BaA—1 sp.]; fossil.
290. *Ripidius* Thunberg, 1806 [BaA—1 sp.]; Recent: Neotropical (N), Oriental, Palaearctic (W). Fig.51.

Family Zopheridae Solier, 1834
291. *Bitoma* Herbst, 1793 [BaA—1 sp.]; Recent: cosmopolitan.
292. *Diodesma* Latreille, 1829 [BaA—1 sp.]; Recent: Palaearctic (W). Fig.52.
293. *Endophloeus* Dejean, 1834 [BaA—1 sp.]; Recent: Oriental (N), Palaearctic (W). Fig.53.
294. *Pycnomerus* Erichson, 1842 [BaA—1 sp.]; Recent: cosmopolitan.
295. *Xylolaemus* Reitter, 1882 [BaA—3 spp.]; Recent: Afrotropical (E), Madagascar, Oriental (N), Palaearctic (W). Fig.54.



FIGURES 49–56. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **49)** *Serropalpus*; **50)** *Glipostena*; **51)** *Ripidius*; **52)** *Diodesma*; **53)** *Endophloeus*; **54)** *Xylolaemus*; **55)** *Isomira*; **56)** *Pentaphyllus*.

Family Tenebrionidae Latreille, 1802

296. *Isomira* Mulsant, 1851 [BaA—1 sp.]; Recent: Holarctic, Neotropical (N). Fig.55.
297. *Mycetocharoides* Schaufuss, 1889 [BaA—1 sp.]; fossil.
298. *Palorus* Mulsant, 1854 [BaA—0]; Recent: Afrotropical, Australian, Madagascar, Oriental, Palaearctic.
299. *Nalassus* Mulsant, 1854 [BaA—1 sp.]; Recent: Holarctic.
300. *Pentaphyllus* Dejean, 1821 [BaA—1 sp.]; Recent: Afrotropical, Australian, Holarctic, Madagascar, Oriental. Fig.56.
301. *Vabole* Alekseev et Nabozhenko, 2015 [BaA—1 sp.]; fossil.

302. *Yantaroxenos* Nabozhenko, Kirejtshuk et Merkl, 2016 [BaA—1 sp.]; fossil.

Family Prostomidae C.G. Thomson, 1859
303. *Prostomis* Latreille, 1825 [BaA—0]; Recent: Afrotropical, Australian, Holarctic, Oriental. Fig.57.

Family Oedemeridae Latreille, 1810
304. *Oedemera* Olivier, 1789 [BaA—0]; Recent: Oriental (N), Palaearctic.

Family Mycteridae Blanchard, 1845
305. *Neopolypria* Abdullah, 1964 [BaA—1 sp.]; fossil.

Family Pyrochroidae Latreille, 1807
306. *Palaeopyrochroa* Abdullah, 1965 [BaA—1 sp.]; fossil.

Family Salpingidae Leach, 1815
307. *Protolissodema* Alekseev, 2013 [BaA—1 sp.]; fossil.
308. *Salpingus* Illiger, 1802 [BaA—1 sp.]; Recent: Australian, Holarctic, Neotropical.

Family Ischaliidae Blair, 1920
309. *Ischalia* Pascoe, 1860 [BaA—1 sp.]; Recent: Nearctic, Oriental, Palaearctic. Fig.58.

Family Anthicidae Latreille 1819
310. *Macratria* Newman, 1838 [BaA—4 spp.]; Recent: cosmopolitan.
311. *Tomoderus* La Ferté-Sénectère, 1849 [BaA—2 spp.]; Recent: cosmopolitan.

Family Aderidae Winkler, 1927
312. *Circaeus* Iablokoff-Khnzorian, 1961 [BaA—1 sp.]; fossil.
313. *Cnopus* Champion, 1893 [BaA—1 sp.]; Recent: Holarctic.
314. *Escalerosia* Nardi, 2007 [BaA—1 sp.]; Recent: Afrotropical, Oriental.
315. *Palaeocnopus* Alekseev et Grzymala, 2015 [BaA—1 sp.; BiA—3 spp.]; fossil.
316. *Picemelinus* Nakane, 1987 [BaA—1 sp.]; Recent: Palaearctic (E).
317. *Vanonus* Casey 1895 [BaA—2 spp.]; Recent: Holarctic.

Family Cerambycidae Latreille, 1802
318. *Clytus* Laicharting, 1784 [BaA—1 sp.]; Recent: Holarctic.
319. *Dicentrus* LeConte, 1880 [BaA—1 sp.]; Recent: Nearctic (W). Fig.59.
320. *Dorcadionoides* Motschulsky, 1857 [BaA—1 sp.]; fossil.
321. *Dorcaschema* Haldeman, 1847 [BaA—1 sp.]; Recent: Nearctic. Fig.60.
322. *Encyclopidonia* Vitali, 2009 [BaA—1 sp.]; fossil.
323. *Eurapatophysis* Vitali, 2016 [BaA—1 sp.]; fossil.
324. *Europsimus* Vitali, 2011 [BiA—1 sp.]; fossil.
325. *Japonopsimus* Matsushita, 1935 [BaA—1 sp.]; Recent: Oriental (N). Fig.61.
326. *Mesalocerus* Vitali, 2015 [BaA—1 sp.]; fossil.
327. *Necydalis* Linnaeus, 1758 [BaA—1 sp.]; Recent: Holarctic, Oriental.
328. *Nothorhina* Redtenbacher, 1845 [BaA—1 sp.]; Recent: Palaearctic. Fig.62.
329. *Obrium* Dejean, 1821 [BaA—1 sp.]; Recent: Afrotropical, Holarctic, Neotropic, Oriental.
330. *Palaeotetropium* Vitali, 2011 [BiA—1 sp.]; fossil.
331. *Paracorymbia* Miroshnikov, 1998 [BaA—1 sp.]; Recent: Palaearctic.
332. *Parmenops* Schaufuss, 1891 [BaA—1 sp.]; fossil.
333. *Pedostrangalia* Sokolov, 1897 [BaA—1 sp.]; Recent: Oriental (N), Palaearctic.
334. *Pogonochaerus* Dejean, 1921 [BaA—1 sp.]; Recent: Holarctic.
335. *Protachryson* Vitali, 2011 [BaA—1 sp.]; fossil.

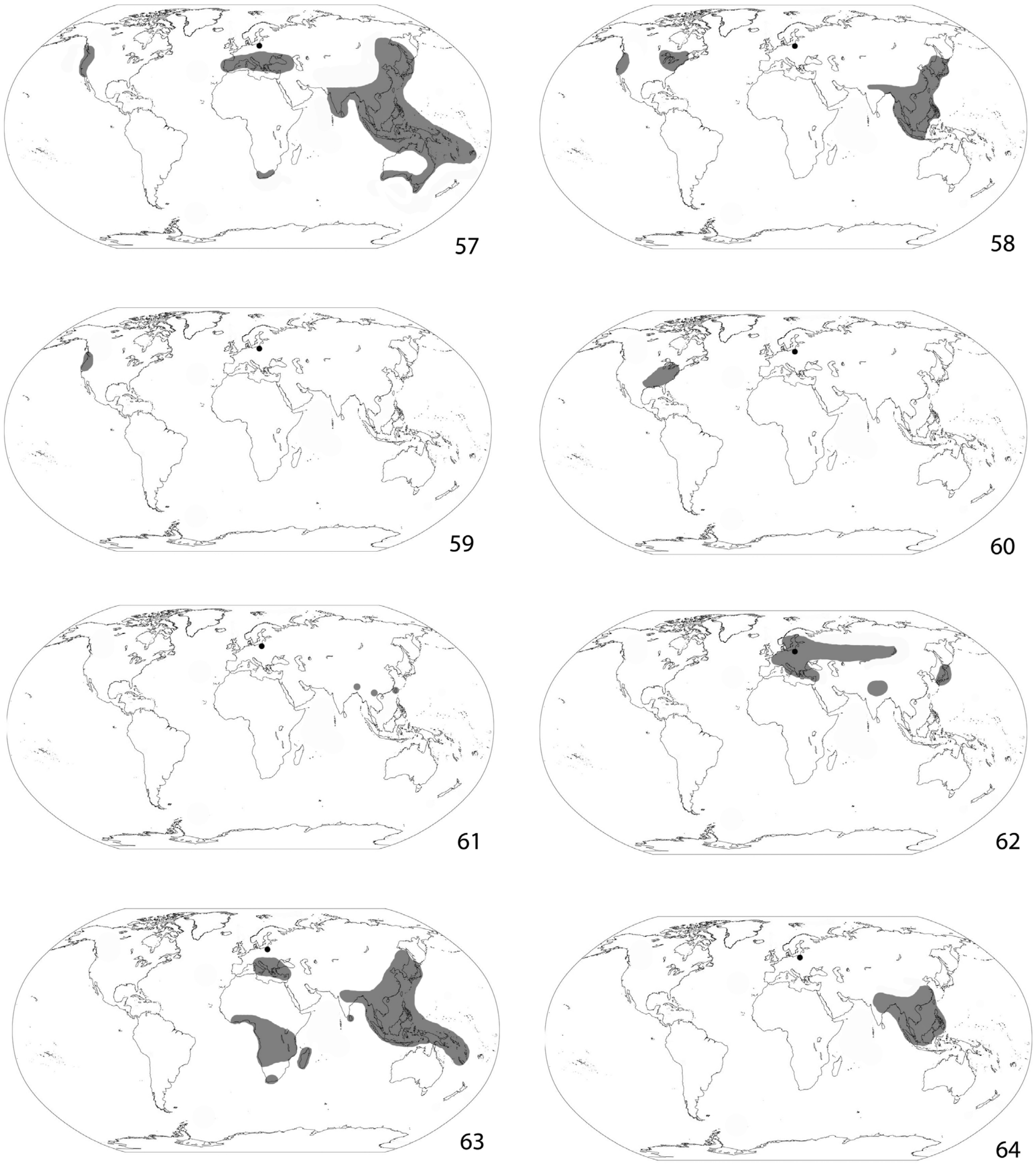
336. *Saphanites* Vitali, 2011 [BaA—1 sp.]; fossil.

337. *Stenhomalus* White, 1855 [BaA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Oriental, Palaearctic. Fig.63.

338. *Strangalia* Audinet-Serville, 1835 [BaA—1 sp.]; Recent: Holarctic, Neotropical.

339. *Tillomorphites* Vitali, 2011 [BaA—1 sp.]; fossil.

340. *Trichosieversia* Vitali, 2009 [BaA—1 sp.]; fossil.



FIGURES 57–64. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **57)** *Prostomis*; **58)** *Ischalia*; **59)** *Dicentrus*; **60)** *Dorcaschema*; **61)** *Japanopsimus*; **62)** *Nothorhina*; **63)** *Stenhomalus*; **64)** *Anisodera*.

Family Chrysomelidae Latreille, 1802

341. *Ambraaltica* Bukejs et Konstantinov, 2013 [BaA—1 sp.]; fossil.

342. *Anisodera* Chevrolat, 1837 [BaA—1 sp.]; Recent: Oriental. Fig.64.
343. *Archealtica* Nadein, 2015 [RoA—1 sp.]; fossil.
344. *Archelamprosomius* Bukejs et Nadein, 2015 [BaA—2 spp.]; fossil.
345. *Calomicroides* Nadein, 2015 [BaA—1 sp.]; fossil.
346. *Calomicrus* Dillwyn, 1829 [BaA—1 sp.]; Recent: Afrotropical, Palaearctic. Fig.65.
347. *Colaspoides* Laporte de Castelnau, 1833 [BaA—1 sp.]; Recent: Australian, Nearctic (S), Neotropical, Oriental, Palaearctic (E). Fig.66.
348. *Crepidodera* Chevrolat, 1837 [BaA—2 spp.; RoA—1 sp.]; Recent: Holarctic, Neotropical, Oriental (N).
349. *Cryptocephalus* Geoffroy, 1762 [BaA—1 sp.]; Recent: cosmopolitan. Fig.67.
350. *Electrocaryedon* Legalov, 2016 [BaA—1 sp.]; fossil.
351. *Electrolema* Schaufuss, 1891 [BaA—1 sp.]; fossil.
352. *Lilioceris* Reitter, 1913 [BaA—1 sp.]; Recent: Australian, Afrotropical, Madagascar, Oriental, Palaearctic.
353. *Manobriomorpha* Nadein et Perkovsky, 2010 [RoA—1 sp.]; fossil.
354. *Oposispa* Uhmann, 1939 [BaA—1 sp.]; fossil.
355. *Paleomolpus* Nadein, 2015 [BaA—1 sp.]; fossil.
356. *Paleophaedon* Nadein, 2010 [RoA—1 sp.]; fossil.
357. *Paolaltica* Biondi, 2014 [BaA—1 sp.]; fossil.
358. *Psyllototus* Nadein, 2010 [BaA—3 spp.; RoA—1 sp.]; fossil.
359. *Succinagonia* Uhmann, 1939 [BaA—1 sp.]; fossil.
360. *Succinispa* Nadein, 2015 [BaA—1 sp.]; fossil.
361. *Succinoomorphus* Bukejs et Nadein, 2015 [BaA—1 sp.]; fossil.
362. *Sucinilivolia* Bukejs, Biondi et Alekseev 2015 [BaA—1 sp.]; fossil.
363. *Taphioporus* Moseyko et Kirejtshuk, 2013 [BaA—3 spp.; RoA—1 sp.]; fossil.

Family Nemonychidae Bedel, 1881
364. *Kuschelomacer* Riedel, 2010 [BaA—1 sp.]; fossil.

Family Anthribidae Billberg, 1820
365. *Allandroides* Legalov, 2015 [BaA—1 sp.]; fossil.
366. *Glaesotropis* Gratshev et Zherikhin, 1995 [BaA—7 spp.]; fossil.
367. *Pseudoglaesotropis* Legalov, 2012 [BaA—1 sp.]; fossil.
368. *Pseudomecorhis* Voss, 1953 [BaA—2 spp.]; fossil.

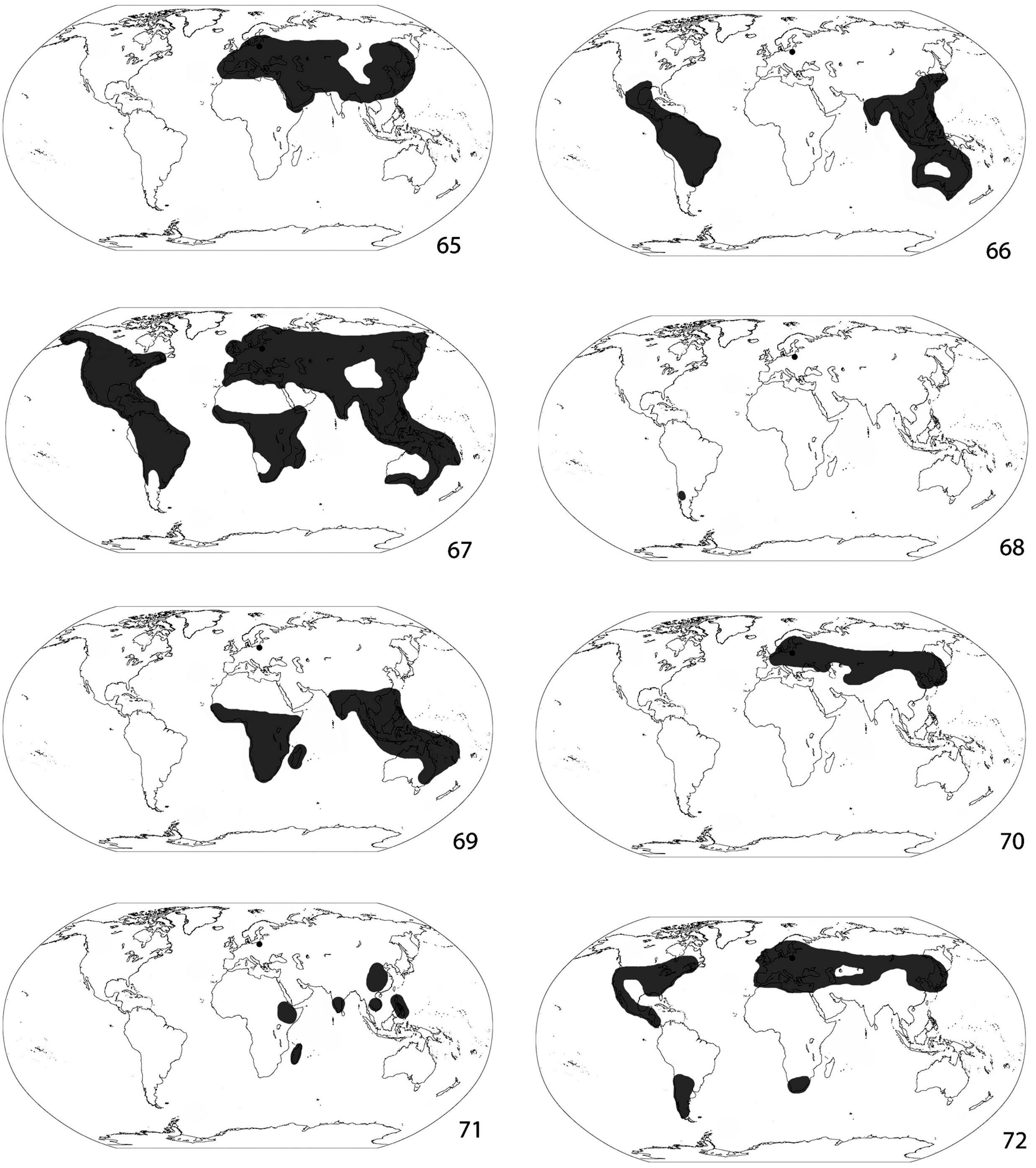
Family Belidae Schoenherr, 1826
369. *Archimetrioxena* Voss, 1953 [BaA—1 sp.]; fossil.
370. *Oxycraspedus* Kuschel, 1955 [BaA—1 sp.]; Recent: Neotropical. Fig.68.
371. *Palaeometrioxena* Legalov, 2012 [BaA—1 sp.]; fossil.
372. *Succinometrioxena* Legalov, 2012 [BaA—2 spp.]; fossil.

Family Rhynchitidae Gistel, 1848
373. *Baltocar* Kuschel, 1992 [BaA—5 spp.]; fossil.
374. *Electrauletes* Legalov, 2015 [BaA—1 sp.]; fossil.
375. *Eocenorhynchites* Legalov, 2012 [BaA—1 sp.]; fossil.
376. *Succinorhynchites* Legalov, 2013 [BaA—1 sp.]; fossil.

Family Brentidae Billberg, 1820
377. *Archinvolvulus* Voss, 1972 [BaA—1 sp.]; fossil.
378. *Conapium* Motschulsky, 1866 [BaA—1 sp.]; Recent: Afrotropical, Australian, Madagascar, Oriental. Fig.69.
379. *Electrapion* Wagner, 1924 [BaA—1 sp.]; fossil.
380. *Melanapion* Wagner, 1930 [BaA—3 spp.]; Recent: Palaearctic. Fig.70.
381. *Pseudaspidapion* Wanat, 1990 [BaA—1 sp.]; Recent: Afrotropical, Madagascar, Oriental, Palaearctic (E). Fig.71.

382. *Stenapion* Wagner, 1912 [BaA—1 sp.]; Recent: Nearctic (S), Neotropical.
383. *Succinapion* Legalov et Bukejs, 2013 [BaA—1 sp.]; fossil.

Family Brachyceridae Billberg, 1820
384. *Thryogenosoma* Voss, 1953 [BaA—1 sp.]; fossil.



FIGURES 65–72. Recent distribution (shaded area) and Eocene fossils (black dot) of genera: **65)** *Calomicrus*; **66)** *Colaspoides*; **67)** *Cryptocephalus*; **68)** *Oxycraspedus*; **69)** *Conapium*; **70)** *Melanapion*; **71)** *Pseudaspidapion*; **72)** *Polydrusus*.

Family Curculionidae Latreille, 1802
385. *Ampharthropelma* Voss, 1972 [BaA—1 sp.]; fossil.
386. *Archaeocallirhipalus* Legalov, 2013 [BaA—2 spp.]; fossil.

387. *Archaeoeugnomus* Legalov, 2016 [BaA—1 sp.]; fossil.
388. *Archaeosciaphilus* Legalov, 2012 [BaA—1 sp.]; fossil.
389. *Arostropsis* Yunakov et Kirejtshuk, 2011 [BaA—1 sp.]; fossil.
390. *Electrotribus* Hustache, 1942 [BaA—2 spp.]; fossil.
391. *Carphoborus* Eichhoff, 1864 [BaA—2 spp.]; Recent: Holarctic.
392. *Caulophilus* Wollaston, 1854 [BaA—2 spp.; RoA—1 sp.]; Recent: Nearctic (S), Neotropical.
393. *Ceutorhynchus* Germar, 1824 [BaA—3 spp.]; Recent: Afrotropical, Holarctic, Neotropical.
394. *Dorytomus* Germar, 1817 [BaA—2 spp.]; Recent: Holarctic.
395. *Eocenesibinia* Legalov, 2016 [BaA—1 sp.]; fossil.
396. *Hylastes* Erichson, 1836 [BaA—1 sp.]; Recent: Holarctic.
397. *Hylurgops* LeConte, 1876 [BaA—6 spp.]; Recent: Holarctic, Neotropical (N).
398. *Leiosoma* Stephens, 1829 [BaA—1 sp.]; Recent: Palaearctic (W).
399. *Necrodryophthorus* Voss, 1953 [BaA—1 sp.]; fossil.
400. *Orchestes* Illiger, 1798 [BaA—1 sp.]; Recent: Holarctic, Afrotropical, Madagascar.
401. *Pachytychius* Jekel, 1861 [BaA—1 sp.]; Recent: Afrotropical, Holarctic, Oriental.
402. *Palaeophelypera* Legalov, 2013 [BaA—1 sp.]; fossil.
403. *Palaeodexipeus* Legalov, 2016 [BaA—1 sp.]; fossil.
404. *Paonaupactus* Voss, 1953 [BaA—3 spp.]; fossil.
405. *Phloeophagus* Schoenherr, 1838 [BaA—1 sp.]; Recent: Afrotropical, Holarctic, Oriental.
406. *Phloeosinus* Chapius, 1869 [BaA—8 spp.]; Recent: cosmopolitan.
407. *Palaeorhamphus* Legalov, 2016 [BaA—1 sp.]; fossil.
408. *Polydrusus* Germar, 1817 [BaA—1 sp.]; Recent: Afrotropical, Holarctic, Neotropical. Fig.72.
409. *Protoceletes* Rheinheimer, 2007 [BaA—1 sp.; RoA—1 sp.]; fossil.
410. *Protonaupactus* Zherikhin, 1971 [BaA—3 spp.]; fossil.
411. *Stenommatomorphus* Nazarenko et Perkovsky 2009 [RoA—1 sp.]; fossil.
412. *Succinacalles* Zherikhin, 1971 [BaA—1 sp.]; fossil.
413. *Succinalophus* Legalov, 2016 [BaA—1 sp.]; fossil.
414. *Succinostyphlus* Kuska, 1996 [BaA—2 spp.]; fossil.
415. *Synommatodes* Voss, 1953 [BaA—1 sp.]; fossil.
416. *Taphramites* Schedl, 1947 [BaA—1 sp.; RoA—1 sp.]; fossil.
417. *Taphrorychus* Eichhoff, 1878 [BaA—1 sp.]; Recent: Oriental, Palaearctic.
418. *Tomicus* Latreille, 1802 [BaA—1 sp.]; Recent: Palaearctic.
419. *Xylechinites* Hagedorn, 1907 [BaA—1 sp.]; fossil.
420. *Xylechinus* Chapuis, 1869 [RoA—1 sp.]; Recent: Afrotropical, Holarctic, Neotropical, Oriental.

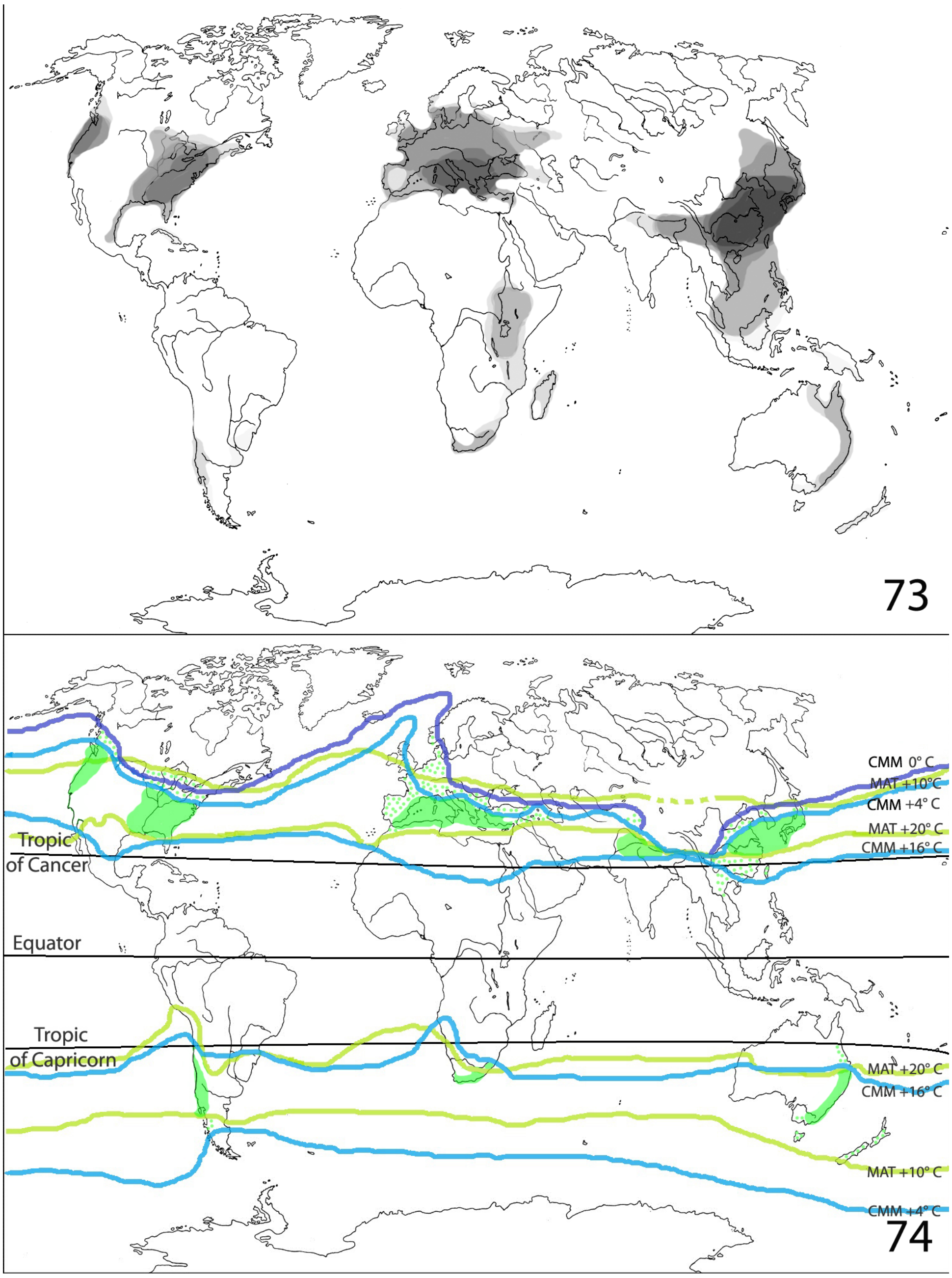
The updated list of beetles from upper or mid-Eocene European ambers includes 420 genera (229 extant and 191 fossil taxa, or correspondingly 54.5% and 45.5% of the total beetle assemblage) from 78 families. Information on the punlished species number within families is provided in Table 1.

Altogether, 614 fossil beetle species have been described from Baltic amber (*s.l.*). The ratio between species belonging to extinct (258 spp.) and extant genera (356 spp.), considering all coleopteran groups together is 0.73 in Baltic amber (*s.l.*). Excluding small families (with 1–2 known genera only), the families with a high proportion of generic palaeo-endemism in the Eocene are: Anthribidae, Rhynchitidae, Lucanidae, Chrysomelidae, Belidae, and Nitidulidae. These groups have comparatively high extinction rates after the period of Baltic amber genesis. On the contrary, Dermestidae, Zopheridae, Latridiidae, Cryptophagidae, Ptiliidae, and Dytiscidae show a remarkable evolutional stasis, and could be declared to be comparatively stable since the Eocene.

No less than 16 other coleopteran families are reported from Baltic amber (*s.l.*), but without description of taxa or reliable generic attribution. These families are: Rhysodidae Laporte de Castelnau, 1840; Hydrophilidae Latreille, 1802; Eucinetidae Lacordaire, 1857; Clambidae Fischer von Waldheim, 1821; Trogidae MacLeay, 1819; Dascillidae Guérin-Méneville, 1843; Byrrhidae Latreille, 1804; Heteroceridae MacLeay, 1825; Cerophytidae Latreille, 1834; Kateretidae Erichson, 1843; Sphindidae Jacquelin du Val, 1858; Cerylonidae Billberg, 1820; Coccinellidae Latreille, 1807; Ciidae Leach in Samouelle, 1819; Meloidae Gyllenhal, 1810; and Megalopodidae Latreille, 1802. The described palaeodiversity of Baltic amber (*s.l.*) is still rather low in terms of the remaining taxa

(Penney 2016). The descriptions of taxa from these (and maybe other) beetle families are expected, and these additions will refine our initial results.

The generalized distributional maps for 72 genera representing 42 families (17.4% of generic diversity) were complied (Figs. 1–72). Several representatives (*Escalerosia*, *Europs*, *Dignomus*, *Diodesma*, *Glipostena*, *Pseudobothrideres*, *Salpingus*, *Tetratoma*, and *Xestipige*) of recent genera in Baltic amber (*s.l.*) are imaged on Fig.75 (A-I); seven beetles of extinct genera from Baltic amber (*s.l.*) are imaged on Fig. 76 (A-G).



FIGURES 73–74. Refugia of the Eocene beetle fauna: **73)** Territories especially rich in surviving Eocene amber beetles (the highest concentration of range overlaps); **74)** The climatically optimal territories and the main climate limitations for the surviving beetle genera from Baltic amber (*s.l.*): blue lines—CMM, the coldest month isotherms (approximately, sea-level, January in the North Hemisphere and July in the South Hemisphere); yellow lines—MAT, mean annual temperatures (approximately, sea-level); green and green-spotted areas—the most appropriate humid climatic territories generally limited by the mean of annual precipitation.

TABLE 1. Beetles diversity in the middle-upper Eocene European ambers (07 March 2017).

No	Family	Number of genera		Number of described species			
		extant	extinct	BaA	RoA	BiA	total
1	Cupedidae	1	1	8	0	0	8
2	Micromalthidae	1	0	0	1	0	1
3	Gyrinidae	0	1	1	0	0	1
4	Dytiscidae	4	0	4	0	0	4
5	Carabidae	8	10	37	0	0	37
6	Histeridae	2	0	2	0	0	2
7	Agyrtidae	1	0	1	0	1	2
8	Leiodidae	3	1	4	1	0	5
9	Ptiliidae	3	0	3	1	0	4
10	Staphylinidae	30	36	84	9	0	93
11	Lucanidae	0	3	3	0	0	3
12	Scarabaeidae	2	0	2	0	0	2
13	Scirtidae	3	3	23	0	0	23
14	Elmidae	2	0	2	0	0	2
15	Limnichidae	0	1	1	0	0	1
16	Ptilodactylidae	0	2	2	0	0	2
17	Buprestidae	1	0	1	0	0	1
18	Schizopodidae	0	1	1	0	0	1
19	Artematopodidae	1	1	6	0	0	6
20	Elateridae	6	7	15	0	0	15
21	Brachypsectridae	1	0	+	0	0	0
22	Eucnemidae	14	3	13	0	0	13
23	Throscidae	4	1	7	0	0	7
24	Berendtimiridae	0	1	1	0	0	1
25	Omalisidae	0	1	1	0	0	1
26	Lycidae	3	1	4	0	0	4
27	Lampyridae	0	2	2	0	0	2
28	Omethidae	0	1	1	0	0	1
29	Cantharidae	6	7	19	2	0	21
30	Jacobsoniidae	1	0	1	0	0	1
31	Dermestidae	9	0	19	1	0	20
32	Bostrichidae	1	0	2	0	0	2
33	Ptinidae	13	3	23	2	0	25
34	Biphyllidae	1	0	1	0	0	1
35	Lymexylidae	0	1	1	0	0	1
36	Trogossitidae	1	1	2	0	0	2
37	Cleridae	8	5	17	0	0	17
38	Dasytidae	2	1	4	0	0	4
39	Malachiidae	1	2	3	1	0	4
40	Cybocephalidae	1	0	1	0	0	1
41	Nitidulidae	1	4	9	0	1	10

......continued on the next page

TABLE 1. (Continued)

No	Family	Number of genera		Number of described species			
		extant	extinct	BaA	RoA	BiA	total
42	Monotomidae	2	0	2	0	0	2
43	Silvanidae	0	2	2	0	0	2
44	Passandridae	1	0	1	0	0	1
45	Smicripidae	1	0	1	0	0	1
46	Phalacridae	1	1	0	1	1	2
47	Cryptophagidae	3	0	2	3	0	5
48	Erotylidae	1	2	1	1	1	3
49	Bothrideridae	1	0	2	0	0	2
50	Anamorphidae	1	0	0	0	0	0
51	Endomychidae	2	2	2	0	0	2
52	Corylophidae	1	0	1	0	0	1
53	Latridiidae	9	1	16	0	0	16
54	Mycetophagidae	0	1	1	0	0	1
55	Tetratomidae	1	0	1	0	0	1
56	Melandryidae	4	3	11	1	0	12
57	Mordellidae	5	1	11	1	0	12
58	Scraptiidae	3	2	9	1	0	10
59	Ripiphoridae	1	2	3	0	0	3
60	Zopheridae	5	0	7	0	0	7
61	Tenebrionidae	4	3	6	0	0	6
62	Prostomidae	1	0	+	0	0	0
63	Oedemeridae	1	0	+	0	0	0
64	Mycteridae	0	1	1	0	0	1
65	Pyrochroidae	0	1	1	0	0	1
66	Salpingidae	1	1	2	0	0	2
67	Ischaliidae	1	0	1	0	0	1
68	Anthicidae	2	0	6	0	0	6
69	Aderidae	4	2	7	0	3	10
70	Cerambycidae	12	11	21	0	2	23
71	Chrysomelidae	6	17	26	6	0	32
72	Nemonychidae	0	1	1	0	0	1
73	Anthribidae	0	4	11	0	0	11
74	Belidae	1	3	5	0	0	5
75	Rhynchitidae	0	4	8	0	0	8
76	Brentidae	4	3	9	0	0	9
77	Brachyceridae	0	1	1	0	0	1
78	Curculionidae	15	21	58	5	0	63
Total		229	191	568	37	9	614

FIGURE 75. Representatives of recent genera in Baltic amber (*s.l.*): **A)** *Xestipyge ikanti* Alekseev, 2016; **B)** *Salpingus henricusmontemini* Alekseev, 2013; **C)** *Pseudobothrideres criwecriwayto* Alekseev, 2015; **D)** *Europs insterburgensis* Alekseev, 2014; **E)** *Diodesma slipinskii* Alekseev et Bukejs, 2016; **F)** *Dignomus regiomontanus* Alekseev, 2014; **G)** *Tetratoma nikitskyi* Alekseev, 2013; **H)** *Glipostena* sp.; **I)** *Escalerosia igori* Alekseev et Grzymala, 2015.

Discussion

1. Zoogeography of the Baltic amber (*s.l.*) beetles.

"What we re-find today in both the northerly world regions, we call the holarctic fauna of the amber, what is re-found only in the old world, is called its palaearctic fauna, and what is found only in North America, is called its nearctic fauna. In reality, they are all merely fragments of the same original fauna from the Palaeogenic age" (Larsson 1978). The zoogeographical inventory of coleopteran fossils is interesting and primarily reflects the regions with more or less effective survival of old taxa. The performed zoogeographical analysis for the 229 modern generic units from Baltic amber (*s.l.*) shows some other key features:

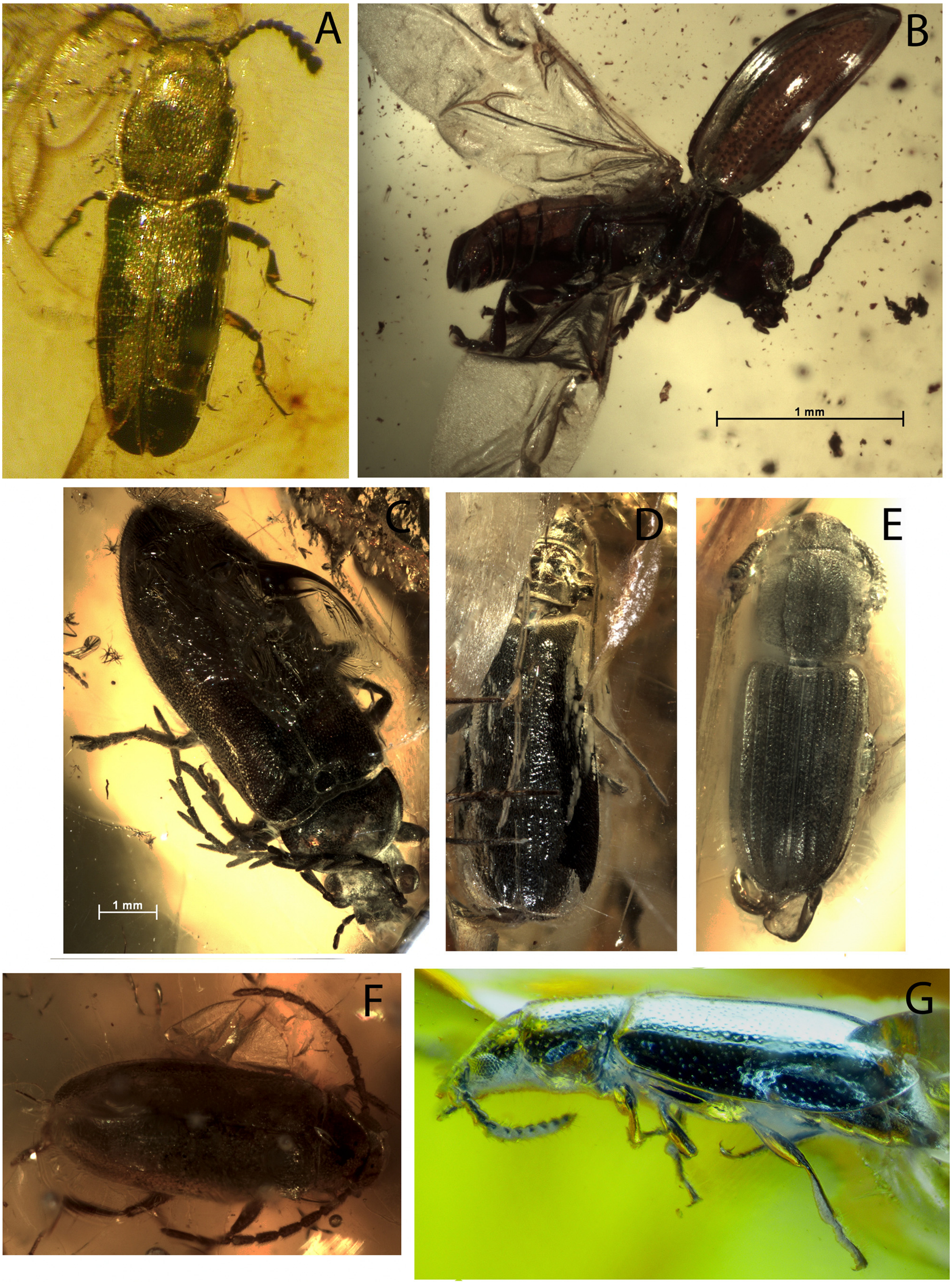


FIGURE 76. Representatives of extinct genera in Baltic amber (*s.l.*): **A)** *Warnis tvanksticus* Lyubarsky, Perkovsky et Alekseev, 2016; **B)** *Sucinolivolia torpida* Bukejs, Biondi et Alekseev, 2015; **C)** *Electrolichas circumbalticus* Alekseev et Jäch, 2016; **D)** *Curche pauli* Alekseev et Kazantsev, 2014; **E)** *Mistran ot* Alekseev et Bukejs, 2016; **F)** *Quasianisoxya curonensis* Alekseev, 2015; **G)** *Protolissodema ulrikae* Alekseev, 2013.

1. The large majority of the Baltic amber (*s.l.*) Coleoptera assemblage consists of Palaearctic inhabitants, represented by 196 genera (85.6% of the total assemblage). The Nearctic inhabitants are conspicuously diverse, with 160 genera (70%), followed by Oriental (140 genera, 61.1%), Afrotropical (115 genera, 50.2 %), Neotropical (105 genera, 45.9%), and Australian (86 genera, 37.6%) zoogeographical elements. If cosmopolitan taxa are subtracted from the count, the number of Eocene genera in realms is slightly different: Palaearctic (140 genera or 80.9 %), Nearctic (104 or 60.1%), Oriental (84 or 48.6%), Afrotropical (59 or 34.1%), Neotropical (49 or 28.3%), and Australian (30 or 17.3%). Surprisingly, the Recent Nearctic fauna of beetles appears to be more similar to the Eocene Baltic biota than to the Recent Oriental one. It is noteworthy that the zoogeographical affinity of the Eocene amber assemblage coincides with the modern system of zoogeographical division of the Earth: Palaearctic and Nearctic are the closest; Oriental, Afrotropical and Neotropical regions are progressively more biogeographically distant from the Holarctic, and the most peculiar fauna belongs to the Australian realm.

2. The overwhelming majority of the listed Eocene coleopteran genera from amber (198 genera, 86.5%) belong to two or more zoogeographical realms at present. They have six-realm or cosmopolitan distributions (56 genera, 24.5 %), five-realm (21 taxa, 9.2%), four-realm (26 genera, 11.4%), three-realm (35 genera, 15.3%), or two-realm (60 taxa, 26.2%) distributions now.

The Eocene taxa that are restricted to one zoogeographical realm (that are more or less local) are comparatively few, being represented by 31 genera (13.5 % of the assemblage). These genera with restricted and possibly relict distributions are: Palaearctic (18), Nearctic (5), Afrotropical (3), Oriental (3), and Neotropical (2) now.

Five taxa (2.2%) of beetles from the Eocene of Europe are known in the Recent from the western part of the Palaearctic only. These genera (*Diodesma*, *Dryophilus*, *Leiosoma*, *Macrocerus*, and *Seidlitzella*) could be true endemics of the western Palaearctic area. The present-day distribution (Figs. 52, 25, 31) and Eocene representatives can be interpreted as a possible "European" origin of these genera. However, the unique role of the eastern Palaearctic as a separate refuge for Eocene taxa of the amberiferous forests is not confirmed indisputably. Almost all Eocene beetles (except for the Japanese endemic *Picemelinus*) that are surviving in the south-eastern and eastern parts of the Palaearctic now have extended distributions (including at a minimum the northen Oriental or Nearctic).

3. In total, 35 extant genera of beetles have gone extinct in the Palaearctic since the Eocene. These genera include: *Adinopsis*, *Aneurops*, *Arisus*, *Balistica*, *Brachypsectra*, *Canifa*, *Caulophilus*, *Ceratus*, *Conapium*, *Cymatodera*, *Derovatellus*, *Dicentrus*, *Dorcaschema*, *Electribius*, *Escalerosia*, *Eucrada*, *Hemiopsida*, *Heterelmis*, *Japonopsimus*, *Lemidia*, *Mastogenius*, *Micromalthus*, *Oxycraspedus*, *Pactopus*, *Petalium*, *Phyllobaenus*, *Potergus*, *Prosymnus*, *Pseudobothrideres, Pseudopallenis*, *Saprosites, Smicrips, Stenapion, Thanasimoides*, and *Xamerpus*. From these 35 genera, 13 genera are restricted to one zoogeographical realm at present (5—Nearctic, 3—Oriental, 3—Afrotropical, 2—Neotropical); 12 genera occur in two realms (7—Nearctic and Neotropical; 2—Oriental and Australian; 2—Afrotropical and Oriental, 1—Neotropical and Australian); 5 genera occur in three realms; 4 genera occur in four realms; and 1 (*Adinopsis*) lives in five zoogeographical realms. In total, out of these 35 genera that are extinct in the Palaearctic realm, 19 (54.3%) can be found in the Recent Nearctic realm, 17 (48.6%)—in Neotropical, 14 (40%)—in Oriental, 13 (37.1%)—in Afrotropical, and 10 (28.6%)—in the Australian realm.

4. Additionally, 26 coleopteran genera are extirpated in Europe since the Eocene but have survived in the eastern Palaearctic. There are: *Abelater, Anisodera*, *Cephennomicrus*, *Colaspoides*, *Coptodera*, *Cupes*, *Discharachthis*, *Euryptychus*, *Falsomordellistena*, *Fornax*, *Glipostena*, *Helcophorus*, *Heterlimnius*, *Hydrotrupes*, *Kolibacium*, *Microscapha*, *Orthrius*, *Phenolia*, *Picemelinus*, *Prionochaeta*, *Pseudaspidapion*, *Pseudoplatopterus*, *Spinifornax*, *Strotocera*, *Themus*, and *Trichodesma*. Among these 26 taxa, 2 genera are cosmopolitan (*Coptodera*, *Fornax*); 7 genera—subcosmopolitan; 2 genera occur in 4 realms (*Cephennomicrus*, *Falsomordellistena*); 5 genera occur in 3 realms; 9 taxa can be found in only one realm (6—in Oriental and 3—in Nearctic); and one genus (*Picemelinus*) is considered to be endemic for the eastern Palaearctic region at present.

In total, 252 coleopteran genera (*i.e.*, 60%) from 420 the middle-upper Eocene list are absent in modern Europe. The greatest part (191 taxa, or 45.5%) of the list is considered to be exclusively fossil and extinct in the modern world fauna, while 61 genera (14.5%) are extirpated only in the western Palaearctic and are non-European at present. Approximately 40% of the beetle genera from the middle-upper Eocene European ambers can still be found in the wild in modern Europe.

5. The distribution of the Baltic amber (*s.l.*) coleopteran genera can be formally categorized according to the number of realms currently occupied by the following groups and subgroups:

1. Widely distributed.

1.1. Cosmopolitan (occurring in all 6 realms)—56 genera, or 24.5% of the assemblage: *Aleochara*, *Anaspis*, *Anthrenus*, *Ataenius*, *Atheta*, *Atomaria*, *Aulonothroscus*, *Bembidion*, *Bitoma*, *Carcinops*, *Cardiophorus*, *Cartodere*, *Clypastraea*, *Copelatus*, *Coptodera*, *Corticaria*, *Corticarina,* *Cryptocephalus*, *Cryptophagus*, *Dermestes*, *Derolathrus*, *Dienerella*, *Diochus*, *Dromeolus*, *Dromius*, *Elaphropus*, *Enicmis*, *Euconnus*, *Euplectus*, *Fornax*, *Holoparamecus*, *Latridius*, *Lathrobium*, *Leptusa*, *Macratria*, *Megapenthes*, *Micrambe*, *Microrhagus*, *Mordella*, *Mordellistena*, *Orchesia*, *Passandra*, *Phloeosinus*, *Poecilochrus*, *Ptinella*, *Ptinus*, *Pycnomerus*, *Sepedophilus*, *Scraptia*, *Stenichnus*, *Stenus*, *Stilbus*, *Tomoderus*, *Trixagus*, *Trochoideus*, and *Trogoderma*.

1.2. Subcosmopolitan (occurring in 5 zoogeographical realms)—21 taxa, or 9.2%;
1.2.1. Subcosmopolitan except for the Palaearctic realm—1 (*Adinopsis*);
1.2.2. Subcosmopolitan except for the Afrotropical realm—4 (*Colaspoides*, *Cybocephalus*, *Diplocoelus*, *Euryptychus*);
1.2.3. Subcosmopolitan except for the Australian realm –7 (*Europs*, *Malthodes*, *Melanophtalma*, *Microscapha, Obrium, Trichodesma, Xylechinus*);
1.2.4. Subcosmopolitan except for the Neotropical realm—7 (*Attagenus*, *Cupes*, *Prostomis*, *Pentaphyllus, Rybaxis*, *Tachyporus*);
1.2.5. Subcosmopolitan except for the Nearctic realm—2 (*Discharachthis*, *Octavius*).

1.3. Distributed in 4 realms—26 genera (11.4%):
1.3.1. Absent in Afrotropical and Australia—5 (*Crepidodera*, *Cyphon*, *Elater*, *Euaesthetus*, *Malthinus*);
1.3.2. Absent in Neotropical and Nearctic—5 (*Cephennomicrus*, *Lilioceris*, *Palorus, Paraphloeostiba*, *Stenhomalus*);
1.3.3. Absent in Oriental and Australian—3 (*Calathus, Ceutorhynchus*, *Polydrusus*);
1.3.4. Absent in Neotropical and Australian—7 (*Gastrallus*, *Mordellaria*, *Pachytychius*, *Phloeophagus*, *Rhagomicrus*, *Trechus, Xestipyge*);
1.3.5. Absent in Afrotropical and Palaearctic—1 (*Brachypsectra*);
1.3.6. Absent in Palaearctic and Australia—1 (*Deravatellus*);
1.3.7. Absent in Palaearctic and Nearctic—1 (*Saprosites*);
1.3.8. Absent in Palaearctic and Oriental—1 (*Mastogenius*);
1.3.9. Absent in Afrotropical and Oriental—1 (*Salpingus*);
1.3.10. Absent in Nearctic and Australia—1 (*Falsomordellistena*).

1.4. Distributed in 3 realms—35 genera (15.3% of the assemblage):
1.4.1. Occurring in the Palaearctic, Nearctic, and Oriental—13 (*Athous*, *Catops*, *Elodes*, *Ernobius*, *Heterlimnius*, *Ipelates*, *Ischalia*, *Limodromus*, *Microcara*, *Necydalis*, *Phyllodrepa*, *Stephostethus, Tyrus*);
1.4.2. Occurring in Palaearctic, Afrotropical, and Oriental—8 (*Aplocnemus*, *Dignomus*, *Evorinea*, *Glipostena, Pseudaspidapion*, *Stenaesthetus, Strotocera*, *Trinodes*);
1.4.3. Occurring in Palaearctic, Nearctic, and Afrotropical—2 (*Chevrolatia, Orchestes*);
1.4.4. Occurring in Palaearctic, Nearctic, and Neotropical—5 (*Hydroporus*, *Hylurgops*, *Isomira*, *Serropalpus, Strangalia*);
1.4.5. Occurring in Nearctic, Neotropical, and Afrotropical—2 (*Phyllobaenus*, *Petalium*);
1.4.6. Occurring in Neotropical, Oriental, and Australian—1 (*Hemiopsida*);
1.4.7. Occurring in Neotropical, Palaearctic, and Australian—1 (*Spinifonax*);
1.4.8. Occurring in Afrotropical, Oriental, and Australian—1 (*Pseudobothrideres*);
1.4.9. Occurring in Palaearctic, Neotropical, and Oriental—1 (*Ripidius*);
1.4.10. Occurring in Afrotropical, Oriental, and Australian—1 (*Conapium*).

1.5. Distributed in 2 realms—60 genera (26.2% of assemblage):

1.5.1. Holarctic (Nearctic+Palaearctic)—33 genera (*Abdera*, *Asiocnemis*, *Bolitobius*, *Cantharis*, *Carphoborus*, *Clytus*, *Cnopus*, *Dorytomus*, *Globicornis*, *Episernus*, *Hemicoelus*, *Hydrotrupes*, *Hylastes*, *Hylis*, *Limonius*, *Loricera*, *Megatoma*, *Micridium*, *Microbregma*, *Nalassus*, *Nemadus*, *Oxyporus*, *Phymatura*, *Pogonochaerus*, *Rhagonycha*, *Vanonus*, *Prionochaeta*, *Pseudoplatopterus*, *Revelieria, Stephanopachys*, *Symbiotes*, *Tetratoma*, *Triplax*);

1.5.2. Palaearctic-Oriental—10 genera (*Abelater*, *Anisodera*, *Endophloeus*, *Helcophorus*, *Kolibacium*, *Oedemera, Orthrius*, *Pedostrangalia*, *Taphrorychus*, *Themus*);

1.5.3. New World (Nearctical+Neotropical)—7 genera (*Aneurops*, *Canifa*, *Caulophilus*, *Cymatodera*, *Heterelmis*, *Smicrips, Stenapion*);

1.5.4. Palaearctic-Afrotropical—5 genera (*Homophthalmus*, *Phradonoma*, *Calomicrus*, *Xylolaemus*, *Colotes*);

1.5.5. Oriental-Australian—2 genera (*Arisus*, *Potergus*);

1.5.6. Palaeotropic (Afrotropical+Oriental)—2 genera (*Escalerosia*, *Xamerpus*);

1.5.7. Gondwanan (Neotropical+Australian)—1 genus (*Lemidia*).

2. Narrowly distributed (inhabiting a single zoogeographical realm)—31 genera, or 13.5 % of the assemblage:

2.1. Palaearctic—18 genera (*Batrisus*, *Bythinus*, *Cephennodes*, *Dictyon*, *Diodesma*, *Dryophilus*, *Faronus*, *Hadrobregmus*, *Leiosoma*, *Macrocerus*, *Melanapion*, *Microptilium*, *Nothorhina*, *Paracorymbia*, *Picemelinus*, *Seidlitzella, Tomicus*, and *Tychus*); from these 5 taxa (*Diodesma*, *Dryophilus*, *Leiosoma*, *Macrocerus*, and *Seidlitzella*) are known now from the western parts of the Palaearctic only, and only one genus (*Picemelinus*) occurs now solely in the eastern Palaearctic;

2.2. Nearctic—5 genera (*Dicentrus*, *Dorcaschema*, *Eucrada*, *Micromalthus*, *Pactopus*);

2.3. Afrotropical—3 genera (*Prosymnus*, *Pseudopallenis*, *Thanasimoides*);

2.4. Oriental—3 genera (*Japonopsimus*, *Balistica*, *Ceratus*);

2.5. Neotropical—2 genera (*Elecribius, Oxycraspedus*).

Surprisingly, the role of the Palaearctic and Nearctic areas for the survival of Eocene genera with restricted ranges (*i.e.,* groups 1.5 and 2, inhabiting one or two zoogeographical realms) is evidently larger than for all of the other near-equatorial and tropical realms combined. The genera with realm-restricted ranges (91 of the units analyzed) are concentrated in the Palaearctic (66 genera, or 72.5% of the assemblage), and Nearctic (45 genera, or 49.5%) realms. The Oriental region has 17 genera of this group (18.6%), Neotropical—11 genera (12.1%), Afrotropical—10 genera (10.9%), and Australian—3 genera (3.3%). These numbers could be interpreted as indicating an important refuge role for the southern parts of Holarctic realm, and the comparative youth of genera from the tropical belt.

It has often been emphasized (Ander 1942; Larsson 1978; Hieke & Pietrezeniuk 1984) that the Baltic amber fauna has a high degree of similarity with the Palaearctic and the Nearctic of the present. The analysis performed supports the dominance of Palaearctic and Nearctic distributional ranges in Eocene amber beetles, and the absence of any "mathematically possible" disjunctions and distributional variants. The latter fact can be explained by the presence of distributional barriers between zoogeographical realms: first at all, by the distance between climatically appropriate zones and by continental drift that has occurred since the Mesozoic. The disjunctive distributional areas of Recent coleopteran genera that are found in Eocene Baltic amber (*s.l.*) are different from one another and they appear to be somewhat accidental in their relevant limits but they can be counted and are not fully random. The similarity of the Baltic amber (*s.l.*) beetle assemblage to the modern southern Palaearctic fauna is the strongest, and Nearctic elements are secondary, while Oriental and Afrotropical region taxa are in third place. The affinity of the beetle assemblage from Eocene amber to the Afrotropical region is comparatively closer than it was supposed earlier (Zherikhin 1970; Hieke & Pietrezeniuk 1984). This fact can be easily explained by the geographical proximity and migration possibilities that existed between Eurasian and African continents in the Paleogene and Neogene (before the modern climatic differentiation).

2. Beetle assemblage of Baltic amber (*s.l.*) and climate.

The compiled list of beetles known from Baltic amber shows the coexistence of beetles whose descendants and relatives are living nowadays in equatorial settings with those from high latitudes. The surviving genera of Baltic amber (*s.l.*) are distributed in almost all climatic zones of the Earth, but are most concentrated in the area between 20˚N and 40˚ N. They are absent in the coldest zones without vegetation (near the polar ice cap), and they are scant in the zones without forest cover and with high thermal oscillations (subarctic, tundra, semiarid and arid climate of steppe and deserts).

At least ten modern cosmopolitan genera (*Atheta*, *Atomaria*, *Bembidion*, *Corticaria*, *Cryptophagus*, *Dorytomus*, *Hydroporus*, *Euaestethus*, *Lathridius*, and *Stenus*) are known also from the Arctic [Holocene of Greenland according to Bennike *et al*. (2000)] and can penetrate beyond the Arctic Circle and occur on the Arctic Ocean coasts (70°0′N and sometimes more, subarctic or subpolar climate, i.e. Dfc type of climate according to the Köppen-Geiger classification). Several genera can be additionally listed by analysis of southern tundra zone and forest-tundra territories (Chernov *et al*. 2014).

About 40% of Baltic amber (*s.l.*) beetle genera can be encountered in modern Europe. No less than 100 genera (about 25%) of beetles from the Eocene amberiferous forests occur in the present-day Kaliningrad region on the Sambian peninsula, near the Baltic amber mine. No doubt, the distribution of these beetles is not relict here and the generic ranges suffered significant changes in the past (maybe more than once), and the modern fauna is formed as result of postglacial re-colonization. The temperate climate of the present-day Kaliningrad region (mean annual temperature nearly +8 ˚C; annual precipitation around 650–940 mm; coldest month temperatures between -2 °C and -4 °C; and hottest month temperatures around +18˚C) should be significantly different from the Eocene conditions.

Thermophilic "tropical" taxa are also present, but are infrequently recorded and distinctly less numerous in Baltic amber (*s.l.*), including: *Anisodera*, *Ceratus*, *Colaspoides*, *Deravatellus*, *Electribius*, *Passandra*, *Pseudaspidapion*, *Pseudobothrideres*, *Pseudopallenus*, *Smicrips*, *Trochoideus*. Modern representatives of the genera *Copelatus*, *Cymatodera*, *Evorinea*, *Glipostena*, *Paraphloeostiba*, *Prosymnus*, *Strotocera*, *Xamerpus,* etc. occur quite widely in both tropical and subtropical climatic zones; while *Calomicrus*, *Diodesma*, *Megatoma*, *Pseudoplatopterus*, *Tetratoma*, *Triplax,* etc. occur in the temperate and the subtropical climatic zones; *Coptodera*, *Dignomus*, *Diplocoelus*, *Elater*, *Gastrallus*, *Ischalia*, *Isomira*, *Lemidia*, *Pentaphyllus*, *Phenolia*, *Phyllobaenus*, *Prostomis*, *Ripidius*, *Xylolaemus,* etc. evidently have no restricted thermal requirements and can be encountered in temperate, subtropical and tropical zones; and representatives of *Cryptocephalus* and some other cosmopolitan taxa also evidently inhabit the wide spectrum of different climates.

The presence of the climate-restricted genera can be considered of primarily importance for a palaereconstruction (indicator-genus approach), or of secondary importance (numerical or assemblage approach). In the latter approach, when certain species do not prevail over other climatic groups, they can be considered as non-determining for the climatic reconstruction (*e.g.*, as relicts of warmer or cooler epoch). However, the abovelisted generic examples seem to be full of contradictions in required climatic conditions. This tends to support the possibility of the persistent coexistence of "now tropical" (thermophilous and at the same time thermotolerant taxa) and "now temperate" (mesotermophilous and thermotolerant, more-or-less adapted to cold winters) elements in one mild equalable climate of the past (see below). In this scenario, the most indicative role should be reserved for genera with really restricted climatic requirements, not widely distributed taxa (tropical or otherwise).

The main problems that face this line of research are the sometimes unclear climatic requirements of modern beetles, and the misleading terminology of the words tropic/subtropic/temperate/nemoral/boreal in relation to beetles and climate in the literature. The debate between researches can originate from geographical or biological senses of the same terms, widely used but not strictly determined in science (Kafanov 2005). In addition, the representatives of one genus can distinctly vary in necessary ecological factors. The majority of boreal and temperate species have very broad thermal requirements (Elias 2000). Some Recent genera have an almost cosmopolitan or very wide distribution in different climatic zones. The modern representatives of many taxa are not completely studied for adequate ecological conclusions. So, the copulation and feeding activities of the overhelming part of temperate climate beetles occur between the temperatures of 5–29˚C (with 15–25˚C preferred, which corresponds to "subtropical" temperature requirements), but examples such as the mating of *Tetratoma fungorum* Fabricius, 1790 in nature have been observed at 4˚C [Pers. obs: Kaliningrad region, 13 January 2013]. Is this an example of a truly cryophilic species? Are the beetles of the same forest that are active in the summer (near 20–25˚C) cryophilic (or "boreal") too? The answer to both of these questions is "No". This has implications for ancient ecosystem reconstructions — could we exactly determine the temperatures of the Eocene forest with data on Recent *T. fungorum*, if the genus *Tetratoma* is reported from amber? It is doubtful: the genus is distributed in Europe, the Caucasus and Transcaucasia, Asia Minor, China, Japan, Northern India, Nepal, Bhutan and North America (Nikitsky 2004, 2016), and its members evidently prefer a milder climate. This leads to the suggestion of a major caveate for the analyses herein. Only approximate conclusions can be made by the analysis of numerous taxa from different groups, but the use of either single or randomly selected genera (or several systematically close genera) should be avoided.

The generalized maps provided here are sufficient for global conclusions, but are rough and inexact for the climate determination of local sampling points (especially for mountain territories with elevation gradients). The possible presence of a diapause in all stages of the life cycle of Coleoptera, and the different duration of diapause in different species of the same genus makes conclusions about the required climatic conditions for a genus approximate and tentative. The presence of diapause for survival of a dry or cold season makes the conditions of insect activity different from the broadly defined local climate in an area. In addition, many beetles have a more-or-less cryptic mode of life, which may limit their usefulness for macroclimatic reconstructions. The adaptive strategies of many beetles are determined by physiological, biochemical and behavioral mechanisms, so many genera have very broad geographical expansions.

The modern geographical areas containing significant concentrations and range overlaps of coleopteran genera from succinite are shown in Fig.73. As the Cenozoic relict genera in this study belong to different families, a phylogenetic explanation can be excluded. Hence climate-associated factors are more probable in determining the overlapping ranges of these relict genera. The modern geographical areas of significant concentrations and their dependence on isotherms and high humidity are shown in Fig.74.

The majority of the Eocene coleopteran genera can be found in the area between the annual isotherms (MAT) 10˚C and 20˚C, which can be considered the optimal temperatures for the surviving members of the coleopteran assemblage from the middle-upper Eocene European ambers. Such climatic conditions mostly correspond to the subtropical and temperate maritime climates of today. The average temperature of the coldest month (CMM) should be an important isotherm (Archibald *et al.* 2010). The majority of the surviving Eocene genera prefer a mean value of the coldest month between 0–16˚C. The effectiveness of a refuge depends on the mean annual precipitation (it should be 750–1500 mm) and this can be evaluated in terms of aridity and continentality of climate: the Eocene beetle genera obviously avoid highly continental, semiarid and arid climates and are not xerophilous.

The preferred climate-distributional analysis for 229 modern genera found in Baltic amber (*s.l.*) was made as part of this study. The preferred climates can be listed in decreasing order of the surviving taxa number (with the climate system given according to the integrative classification by Lauer-Frankenberg):

1. B_3sh (subtropical maritime semihumid) and B_2sh (subtropical continental semihumid);
2. B_3h (subtropical maritime humid), B_2h (subtropical continental humid), C_{I3}sh (warm temperate maritime semihumid);
3. A_1 and A_2 (cold and warm tropical consequently), C_{I3}h (warm temperate maritime humid), C_{I2}h (warm temperate continental humid), C_{I2}sh (warm temperate continental humid).

The almost avoided or totally avoided climates are the following: B_1 (subtropical highly continental), B_2sa and B_2a (subtropical continental semiarid and arid), B_3sa and B3a (subtropical maritime semiarid and arid), C_{II} (cold temperate), D (polar).

According to the effective classification of Köppen-Geiger, the climates preferred by Eocene coleopteran relicts are of the Cf-type (Cfb, Cfa, Cfc). These climates are temperate, without a dry season, with temperatures of the hottest month higher than 10˚C and temperatures of the coldest month between 0 and 18˚C. However, the appropriate climates for several taxa are Dfa, Dfb (cold, without dry season), Dwa, Dwb (cold, with dry winter), Cwa (temperate, with dry winter), Csb (temperate, with dry and warm summer), Aw (tropical savannah). Various B-type (arid) and E-type (polar) climates are almost entirely avoided.

Summarizing the data obtained from both classifications, the places preferred by the majority of Eocene coleopteran genera have modern “semihumid subtropical, humid subtropical or warm temperate semihumid” climates (according to Lauer-Frankenberg), or “temperate, without dry season” climate (in accordance with the Köppen-Geiger system). Our conclusions generally correspond to Andrée (1951): “die Insektenfauna spricht für ein warmgemäßiges Klima mit an thermisch günstiger gelegenen Orten subtropischen Einschlag" [The fauna of insects denotes the warm temperate climate with subtropical grade on thermally favorable places] or to Muona (1993): "the climate of the area has been either temperate or subtropical—the latter being perhaps more likely".

Like the exceptional importance of the monophagous plant feeders for plant community reconstructions, the relict genera that are territorially restricted to one area (or to some small, isolated areas) play a great role for conclusions about climate in the Eocene amber forests. Such taxa could be climatically sensitive and could play role of climate indicators. The relevant taxa for our reconstruction are 31 coleopteran genera that occur in one realm (18 Palaearctic, 5 Nearctic, 3 Afrotropical, 3 Oriental, and 2 Neotropical). About three-quarters of these genera are Cf-climate-inhabitants, while several occur also in D-climate or A-climate conditions. In fact, the sample of genera with restricted ranges is in full agreement with the generally calculated climatic preference of the studied assemblage.

The following conclusion can be made on the basis of the general analysis of the whole beetle assemblage, and this conclusion can be supported using the territorially restricted genera. The modern representatives of the surviving Eocene coleopteran genera allow the reconstruction of a warm temperate, humid, equable climate with:

1. Annual average temperatures (MAT) between 10 and 20˚C (probably 14–16˚C);
2. Mild winters, with a mean of the coldest month temperatures possibly around 10˚C (between 4˚C and 16˚C); however, possible winter lows below 0˚C are not excluded;
3. Annual temperature range small, thermal seasonality reduced (less than 15˚C), with a mean hottest month temperature around 20–24˚C;
4. Annual precipitation high, around 750–1500 mm per year, and distributed fairly evenly over the year, but with probable presence of two seasons (summer and winter) with slightly different regimes of precipitation.

Such equable climatic conditions (named humid subtropical or oceanic warm temperate in modern classifications) would be appropriate for almost all beetle genera found in Baltic amber (*s.l.*). Under such conditions, Wheeler's dilemma (Archibald & Farrell 2003) and "such puzzling mixture of termophilous and temperate elements" (Zanetti *et al*. 2016) can be solved for beetles and, maybe, for all insects. The distributional ranges of the Eocene genera are thermally limited by effective temperatures (reflected by annual isotherm), and by the temperatures of the coldest month. Humidity is also extremely important in explaning the distribution of relict genera at present. As pointed out by Kennedy (1993), non-availability of moisture is a more limiting factor than low temperatures to biological activity. Tolerance to low temperatures and resistance to desiccation are overlapping adaptations (Ring & Danks 1994). The contraction of coleopteran distributional ranges was probably caused by the drying trend along with global cooling. The significance of high humidity for Eocene biota was pointed out by Alekseev (2016).

Traditionally (Weitschat & Wichard 1998; Archibald & Farrell 2003), the following groups of insects in Baltic amber (*s.l.*) are considered the best truly "tropical" examples: Blattodea (including termites), Mantoidea, Embiodea, and Phasmatodea. These groups are much more abundant in the modern tropics (in all senses), and are more or less latitudinally limited. However, the temperature threshold of development and dependence on truly tropical climate is somewhat overstated: termites (Scheffrahn *et al*. 2015) reach 54°3′N in Canada (*Zootermopsis angusticollis*) and can occur in areas with a MAT of 4° C (*Reticulitermes* sp.); representatives of Mantodea do not occur farther north or south than 45–46° latitude in either hemisphere (*e.g.,* 51°0′N in Germany); Embiodea reach Crimea; while Phasmatodea occur in the Russian Far East, southern Canada, New Zealand and the Mediterranean area. For all of these insects, the conditions of modern Cfa or Cfb climate types are enough to support stable populations for tens of species. The most thermophilic beetles of Baltic amber (*s.l.*) (representatives of Paussinae as well as the genera *Trochoideus*, *Passandra*, *Pseudobothrideres* and some others) can occur in the above-mentioned climatic conditions too, with exemplars in the lowlands of eastern Asia, southernmost Africa, or south-eastern North America, and also in mountain areas nearer the equator (500 to 2000 m a.s.l. in the Himalayas, northern Malesia, and south-eastern Asia, Madagascar, western South America, and Central America). Consequently, the low thermal seasonality of Eocene Fennosarmatia appears to be the main reason for the mix of present-day latitudinally dispersed beetles and the hight biotic diversity.

According to Alekseev & Alekseev (2016), the Baltic amber forest was formed on a plain or slightly hilly area. These regions were probably vast coastal lowlands. The present-day distribution of many arboreal groups in mountains is a recent characteristic only (Alekseev & Bukejs 2016). A uniform (possibly gradually cooling northwards), warm temperate, humid, equable climate is suitable for developing the community of beetles found in the amberiferous forest of Eocene Europe (the closest modern analogues are often called "coastal", "oceanic" or "maritime"). The amber forest of the middle-upper Eocene Fennosarmatia could be generally classified as a forested wetland on a non-peat substrate, or a wetland-associated habitat.

Several researchers have supposed (Larsson 1978) and argued (Schmidt et al. 2016a, 2016b) for the mountain character of the amber-producing forest, with its mixed fauna originated from multiple source altitudes. The altitudinal gradient could be used as an explanation for the modern ranges of several Eocene beetles in present-day equatorial latitudes (with *de facto* warm temperate humid climate), but its use for explanations in the Eocene amberiferous territory is limited: it is not supported by geological data (mountains are unknown in Fennosarmatia, except for the narrow areas of the Scandes in west and of the Urals in east), and this terrain does not fit with the hypothesized mode of amber deposit accumulation (a result of lowland inundation by sea at the end of the Eocene). Mountainous areas provide a wide array of sheltered habitats where conditions are often milder and moister. In tropical mountainous regions, the comparatively low MAT values are also combined with low seasonality. Somethat similar climate (humid, equable) of the amberferous forest can not directly indicate the orography and can be caused by different reasons. The altitudinal gradient in mountainous areas allows species to shift their distributions during climatic changes (especially by warming and increased aridity of the area), but the mountains cannot serve as refugia during glaciations. There are no specifically mountainous beetles found as inclusions in succinite—apart from *Ipelates*, which is humidity-dependent and restricted to slopes; and a *Trechus* species, which is evidently endogenous, flightless, and anophthalmous.

The discussion about tropical/subtropical or warm-temperate Eocene climate (Andrée 1951; Weitschat & Wichard 1998) could possibly be solved by an exact climatological definition of the terms "subtropical" and "temperate". However, the true tropical belt (equatorial climate and "astronomical tropics" between 23.5° N and 23.5° S) was not accurately defined in the case in the Eocene amber forests. It could be assumed that the main limiting factor for the richness of Eocene beetle genera observed in modern faunas is the coldest month temperatures in the high latitudes of the present-day Northern Hemisphere, whereas the main limiting factor for the present-day Southern Hemisphere and low-latitudinal North Hemisphere is precipitation (the presence of a short dry season, or full absence of droughts). The possible paratropical character (*e.g.*, Szwedo 2008) of Eocene Baltic amber forests is not confirmed in our study.

One other essential point should not be overlooked in the paleoclimatic reconstruction of the European Eocene: the influence of glaciation in the comparatively recent time, and the attendant post-glacial recolonization process (which may be incomplete in the high-latitude regions of Europe) (Baselga *et al*. 2012). The maximum extent of ice sheets in the Northern Hemisphere (24,500 to 17,000 years BCE) pushed the deciduous and mixed forests and their inhabitants southwards, and strongly influenced the humid terrestrial zones around the Earth. A thousand times more recent (in comparison with the tens of millions of years in the Paleogene and Neogene), the European Eocene beetles only occupy a range extending from ~40°0′N and southwards in Europe and East Asia, and ~30°0′N and southwards in North America. The high concentration of relict Eocene genera in this modern "subtropical" or "warm-temperate" area may have accentuated the historically relict characteristics that are thought to exist within these groups. For a wide range of European beetle taxa, dispersal ability is a good predictor of the strength of their latitudinal richness gradients (Baselga *et al.* 2012). The relict distributional patterns may indicate the glacial refugees and low dispersal ability in the first place, but the differences between modern distributional patterns of various Eocene relict taxa cannot be fully explained by Quaternary glaciations alone.

The presented macroclimatic reconstructions of the European Eocene conditions and their impact on the beetle assemblage found in Baltic amber (*s.l.*) are not exact and fully detailed yet. The conclusions about the climate of the Eocene European amberiferous forests should be verified with additional results obtained from analysis of perennial plants and other insect groups. Approaches to estimating paleotemperature with macroflora, such as CLAMP (Climate-Leaf Analysis Multivariate Program), LMA (Leaf Margin Analysis), or palynological study should be used. In general, the suggestion made by previous authors (*e.g.*, Wolfe 1995; Archibald & Farrell, 2003; Archibald *et al*. 2010; Huber & Caballero 2011; Archibald *et al.* 2014) of the greater uniformity within the Eocene climate (greatly reduced meridional temperature gradients) and smaller seasonal temperature differences (substantially warmer mean annual and cold season continental temperatures) is in accordance with our results. High humidity in parts of the Baltic amber forest area is also suggested by abundant amber inclusions of sooty moulds (Schmidt *et al*. 2014), by epiphyllous fungi (Kettunen *et al*. 2015), and by several floristic data (Sadowski *et al*. 2016).

3. Age estimations of extant genera from Baltic amber (*s.l.),* migration routes and continental drift.

Despite the amount of work that has been done on Baltic amber, the paleontological data are certainly not complete, and the time for descriptive taxonomy of Baltic amber (*s.l.*) inclusions has not passed. For 229 Recent genera of beetles, a minimal Eocene age can be declared at the moment (see above in the section "Results"). These genera have different Recent distribution areas, which are also addressed (the first paragraph of the section "Discussion"). The modern distribution of surviving genera is mostly determined by the appropriate climatic conditions (the second paragraph of the section "Discussion"). The differences in present-day areas of the coeval Eocene European beetles and variability of their ranges can be explained by different reasons (in the opinion of the author, these can be explained mostly by extinctions) and are discussed here.

Several Baltic amber coleopteran genera have very interesting and peculiar modern disjunctive distributions. Some of them could be explained by the generic place of origin and possible migration routes in/from Europe or by continental drift. For such cases the hypothetical estimations of the taxon age could be made too. For example, the present-day distributions referred to as Gondwanan or Notogean (southern Neotropical and Australian: *Lemidia,* Fig. 33), and findings in Eocene Europe (as well as present-day cosmopolitan or near cosmopolitan disjunctive distributions) can be interpreted as the most ancient taxa (separation of South America and the Holarctic took place ~135 Ma). The present-day Palaeotropical (Afrotropical+Oriental: *Ceratus*, *Strotocera*, *Xamerpus*, *Ceratus:* Figs. 15, 37, 38) or Palaeotropical-European distribution (Figs. 22, 24, 54, 63), and findings in the Eocene Europe can be interpreted as approximately 84 Ma in age (the age of the division for the Africa-Madagascar-Indian continental mass). Such speculations are possible, but may be open to criticism, and consequently have little predictive value. The endemism of "Gondwanan" type (and any other apparent geologically induced disjunctions) is not a result of the break-up of Gondwana, but rather a relict area due to post-Eocene exinction events.

A good example of this phenomenon is the report of the now endemic for Madagascar clerid genus in Baltic amber (*Pseudopallenis*: Fig. 36), which if viewed in isolation can produce bizarre distributional hypotheses concerning drift of the Gondwanan fragments and discussion concerning the prolonged Mozambiquean sea strait as an effective barrier for beetle migrations. But the coeval genera that also occur on Madagascar (*Mastogenius*, *Pentaphyllus*, *Phradonoma*, *Stenhomalus*, *Xylolaemus* — a buprestid, tenebrionid, dermestid, cerambycid, and zopherid respectively: Figs. 10, 22, 54, 56, 63) show variable and gradual contraction of what was initially a wide and most likely continuous distribution in the Old Word. In the context of the other genera, the enigmatic *Psedopallenis* distribution can be treated as particular case, and only as one of the possible final stages of the range reduction. Such data interpretation is only possible through comparison of taxa from different families — a comparison that is strongly advocated herein. Such a point of view (repeated faunal changes between Asia and Africa, with the possibility of the direct dispersal from Africa to Madagascar) can be supported by the study of the diverse modern African and Malagasy representatives of *Paussus* (Paussinae) (e.g., Moore & Robertson 2014).

Equally, the various disjunctions in Northern Hemisphere (western and eastern North America-Europa-Eastern Asia) in different groups (*Dicentrus*—Fig. 59, *Dictyon*—Fig. 7, *Eucrada*—Fig. 26, *Heterlimnius*—Fig. 8, *Hydrotrupes*—Fig. 4, *Ipelates*—Fig. 6, *Ischalia*—Fig. 58, *Microbregma*—Fig. 29, *Revelieria*—Fig. 46, *Pseudoplatopterus*—Fig. 19) cannot show Transberingian, De Geer (through Fennoscandia) or Thulean (through Iceland, the Faroe Islands and Great Britain) land bridges or land connections in/after/before the Eocene between fragmented continents as was discussed by Gómez & Damgaard (2014). Such phenomena should be interpreted as a continuous and zonal distribution of the taxa in the North Hemisphere in the past. The biota of that time was likely uniform from west to east throughout, at least to the extent that the exact migration routes cannot be ascertained, and the search for possible "more important" transcontinental connections is doomed to failure. The original and interesting hypothesis by Szwedo (2008) concerning the Eocene division of the Northern Hemisphere by epicontinental seaways into two biogeographic regions of which one was western North America plus most of Asia, and the other eastern North America plus Europe unfortunately cannot be confirmed by modern distributions of Eocene beetles from succinite. An epicontinental seaway (the Turgai strait) probably restricted the normal dispersal between Europe and Asia at least some of this time (Archibald *et al*. 2011), but the moderate number of Eocene beetle genera supporting this hypothesis (*Aneurops*—Fig. 40, *Cymatodera*—Fig. 32, *Dicentrus*—Fig. 59, *Diplocoelus*—Fig. 30, *Dorcaschema*—Fig. 60, *Electribius*—Fig. 11, *Eucrada*—Fig. 26, *Micromalthus*—Fig. 2, *Pactopus*—Fig. 16, *Revelieria*—Fig. 46 etc.) is almost equal to contradictive distributional patterns (*Anisodera*—Fig. 64, *Calomicrus*—Fig. 65, *Ceratus*—Fig. 15, *Dictyon*—Fig. 7, *Helcophorus*—Fig. 17, *Japonopsimus*—Fig. 61, *Kolibacium*—Fig. 18, *Strotocera*—Fig. 37, *Trinodes*—Fig. 23, etc.), which show the number of shared elements between Fennosarmatia and modern Asia only. It is noteworthy that representatives of *Smicrips* with a restricted Neotropical distribution at present (Fig. 42), and two Eocene-aged species from Europe could be examples confirming the above-mentioned opinion. However, this genus was recently discovered in Cenomanian Burmese amber (Cai & Huang 2016). Consequently, the wide-ranged distribution in the past (including Asia) is evident now: for discussions about concrete dispersal routes in the Northen Hemisphere in the Eocene, this genus should be regarded as nonsignificant. In the author's opinion, the modern disjunction "Eastern Asia—North America" is typical for Eocene genera, and it can be indicative of the relict character and highly probable presence of a modern taxon in the Eocene time of Fennosarmatia. This disjunction is typical, but not obligate; the gapless distribution in the Holarctic, or ranges with different insular patterns in Northern Hemisphere, can also occur among the surviving Eocene genera.

Examining larger datasets of fossil and modern beetle distributions allows us to improve our biogeographic interpretations. Statements such as the "Baltic amber fauna of Eucnemidae consisted of true Laurasian genera and several Gondwanan ones … and their presence in the Northern hemisphere suggest arrival by invasion through Central America to the Holarctic" (Muona 1993) need to be re-examined. The modern Laurasian or Gondwanan distribution and diversity should not signify the place of origin; the new fossil findings could help to correct and add new data to the distributional picture of a genus. The older age of the Baltic amber specimen could suggest for example: (1) contrary invasion in the Southern Hemisphere from the Holarctic; (2) extinction in the Holarctic of a previously widely distributed (or cosmopolitan) genus with an unclear origin. The assemblage of the Baltic amber forest was heterotopic (consisting of autochthonic and allochthonic taxa) and heterochronous (consisting of taxa of different ages and on different degrees of range formation). It is no wonder that different components of this biota have different fates (extinction/range restriction/wellbeing). "One of the main factors determining the distribution of a group is the distribution of its immediate ancestor" (Heads 2015). The Palaeoeuropean distribution of several groups now restricted to Southern America, Australia, New Zealand and other extremely distant points of Earth should indicate the essential caution for conclusions based on modern material, when making statements about localized centres of the group's origin. Extinctions among groups that were widespread in the past are possibly more important for understanding present-day distributional patterns of Eocene genera than observations of origination points or the virtual directions of migrations based on crown group systematics. One confirmation for such a statement is the modern distribution of *Protopaussus* Gestro, 1892 (south-eastern Palaearctic and Oriental) which has been described from Miocene Dominican amber (Hispaniola) (Nagel 1997). The temporal and geographical distribution of *Protopaussus* indicates that its present zoogeographical range represents the relict of a wide Laurasian distribution in the past, and it does not support the previously suspected Oriental centre of origin (Nagel 1997).

A significant part of the beetles reported from succinate have a mosaic or continuous cosmopolitan distributional range now. There are numerous taxa with subcosmopolitan or multiregional distributions. At present, it is not possible to eliminate from consideration the possibility of the past cosmopolitan distribution of all genera. Such a continuous distribution is the simplest mode to explain the present-day variety of disjunctions. The Recent distributional ranges with isolated parts are not the effect of the age, migration routes and places of origin of each taxon. They result from peculiarities of the modern climatic picture, and the scattered areas of what were continuous climatic zones in the past. The number of groups surviving within a certain territory depends on the modern climate (*i.e.*, similarity to the past one), on geographical proximity of compared points, and on the stability of ecosystems (the age of the modern climate conditions, and presence of dramatic changes in the last, geologically small period of time).

Taking into account the results of this study, it is considered impossible to find non-speculative and well-grounded estimates of taxon age when the recent and past occurrence of the taxon and correlations with continental drift distributional routes of genera are considered as the sole sources of information. The data obtained here are in general agreement with the summarized thesis of K. Eskov (1984): (1) the modern distribution of taxa weakly reflects the zoogeographical history of the group; (2) disjunctions are the remains of wide distributions in the past; (3) the refugia of surviving taxa are determined by climatic reasons; (4) the ability to migrate by insects is higher than expected.

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