

Dynamics of Insect Diversity during the Early and Middle Permian

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Received June 15, 2014

Abstract—The composition of insect families in the Early and Middle Permian is analyzed to reveal the dynamics of taxonomic diversity using the approach developed earlier (Aristov et al., 2013). The efficiency of the methods used for quantitative estimation of the degree and direction of changes is confirmed using 15 sequences of local and, in some cases, regional insect assemblages of Eurasia and North and South America. It is shown that changes that took place at the principal boundaries between the Asselian and Sakmarian, Kungurian and Ufimian, and Early and Late Kazanian were stepwise. At each of these boundaries, the family composition of insects underwent stepwise rejuvenation. Furthermore, the Asselian stage is characterized by dramatic dominance of positive over negative changes in the taxonomic composition of assemblages (i.e., there are more first appearances than last appearances of families) and by low relative (per family) degree of changes. At the next, Artinskian–Kungurian stage, changes in composition stabilize at a moderately positive level and the relative total degree of changes increases. In the Urzhumian–Early Kazanian time, negative changes (i.e., last appearances) predominated; during the Late Kazanian–Urzhumian stage, changes become balanced. Importantly, the negative character of changes that took place during the Ufimian–Early Kazanian time resulted from deceleration of diversification (decrease in the number of first appearances of families) rather than from intensification of extinction (increase in the number of last appearances); we described a similar pattern for the Vyatkian Time of the Late Permian (Rasnitsyn, 2012; Rasnitsyn et al., 2013; Aristov et al., 2013). The relative total degree of changes in the Ufimian–Urzhumian time decreases almost to the Asselian level. It is proposed that not only an increase but also decrease in biological diversity is essentially endogenous, i.e., determined mostly by the specificity of organisms rather than external factors.

Keywords: Insecta, Early and Middle Permian, dynamics of the taxonomic diversity, extinction

DOI: 10.1134/S0031030115120102

INTRODUCTION

Recent studies on the dynamics of taxonomic diversity of insects prior to the Paleozoic–Mesozoic boundary and at this boundary (Rasnitsyn, 2012; Rasnitsyn et al., 2013; Aristov et al., 2013) yielded results so important and unexpected that it was necessary to expand such studies to encompass other stages of the history of insects, including less dramatic ones, with a double purpose: to learn more about the evolution of this extremely important taxon and test using different material the methods developed for studying the dynamics of diversity. The results of the new study are given in this publication.

The studies mentioned have shown that accumulated data on the insect fauna can be adequate to quite ambitious goals. In particular, for the interval analyzed in those publications, the Urzhumian to Induan stages of the Middle and Late Permian and the very basal Triassic, we managed to describe several important

aspects of the dynamics of diversity, such as changes in the total diversity of insect families, the rate of these changes, dynamics of their direction (ratio of positive and negative processes), and changes in the aspect of faunas in terms of the proportions of families considered “ancient” and “young.” In particular, it was revealed that such changes were essentially uniform on the global scale and depletion of the insect fauna took place prior to the Permian–Triassic boundary rather than at this boundary and was caused by a decreased rate of diversification (new families almost ceased to appear) rather than mass extinction. In addition, methods were developed that allow the sequences of fossil assemblages in time to be improved and, hence, are of interest as stratigraphic tools.

We selected as the new subject of such studies the insects of the Early and Middle Permian (Asselian to Urzhumian ages), since it proved possible to accumulate a sufficiently large pool of data about them (over

200 families of 13 assemblages broadly representing Laurasia and unfortunately more poorly representing Gondwana). This allowed us to employ without considerable problems all the methods used earlier and to obtain results that are probably less revolutionary but quite meaningful and useful.

MATERIAL

The data on the insect families analyzed in this study are summarized in Table 1; the data on the occurrence of these families are summarized in Table 2. The composition and origin of assemblages used in our calculations are given below.

Carrizo Arroyo. United States, New Mexico, Valencia County, Carrizo Arroyo locality (outcrops NMMNH L-3433 and 3437); Lower Permian, basal Wolfcampian (Asselian) Stage, Burzum Formation, Red Tanks Member (Schneider and Lucas, 2013).

The checklist of insects is based on Rasnitsyn et al. (2004), unless specified otherwise.

Order Machilida. Family Dasyleptidae (Rasnitsyn et al., 2004).

Order Odonata. Family Luiseiidae (Nel et al., 2012).

Order Caloneurida. Families Caloneuridae and Haplopteridae (Rasnitsyn et al., 2004).

Order Hypoperlida. Family Ischnoneuridae (Rasnitsyn et al., 2004; Rasnitsyn and Aristov, 2013).

Order Dictyoneurida. Families Dictyoneuridae, Calvertiellidae, Spilapteridae, and Hanidae (Kukalová-Peck and Peck, 1976; Rasnitsyn et al., 2004).

Order Diaphanopterida. Families Asthenohymenidae and Martynoviidae.

Order Psocida. Family Psocidiidae.

Order Hemiptera. Family Archescytinidae.

Order Palaeomanteida. Family Palaeomanteidae (Rasnitsyn et al., 2004).

Order Eoblattida. Family Cheliphlebiidae (Aristov, unpublished data).

Order Cnemidolestida. Family Spanioderidae (Aristov, 2014).

Order Gylloblattida. Families Liomopteridae and Probnidae (Aristov, in press).

Order Blattida. Families Phyloblattidae and Poroblattinidae (Schneider et al., 2004).

Order Orthoptera. Family Thuringoedischiidae.

Asselian deposits of Europe. Germany; Meisenheim Formation (=Lebachian Beds), Lower Rotliegend, Lower Permian. Insects come from the following localities: Schwarzenbach, Humberg, Odernheim, Niedermoschel, and Breitenbach in Rheinland-Pfalz (Brauckmann, 1991, 2007; Béthoux and Poschmann, 2009; Prokop et al., 2012), and Steinbach in Hesse (Aristov, 2014). Czech Republic; Padochov Formation. Insects come from the Zbýšov and Říčany local-

ities in the Brno-Venkov District, southern Moravia (Stamberg and Zajíc, 2008).

Order Blattinopseida. Family Blattinopseidae (Brauckmann, 2007; Stamberg and Zajíc, 2008; Prokop et al., 2012).

Order Ephemerida. Family Mithodotidae (Brauckmann, 2007).

Order Dictyoneurida. Families Eugereonidae (Brauckmann, 2007) and Calvertiellidae (Stamberg and Zajíc, 2008).

Order Palaeomanteida. Family Palaeomanteidae (Brauckmann, 2007).

Order Coleoptera. Family Tshkardocoleidae (Brauckmann, 2007).

Order Trichoptera. Family Protomeropidae (Stamberg and Zajíc, 2008).

Order Eoblattida. Family Protophasmatidae (Béthoux and Poschmann, 2009; Aristov, in press).

Order Grylloblattida. Family Permuliidae (Aristov and Storozhenko, 2011), Lemmatophoridae (Brauckmann, 2007; Prokop et al., 2012).

Order Blattida. Families Phyloblattidae (Brauckmann, 2007; Stamberg and Zajíc, 2008), Spiloblatinidae, Mylacridae, Poroblattinidae (Stamberg and Zajíc, 2008), Archimylacridae, and Compsoblattidae (Breitenbach locality: *Paleobiology Database*, 2014).

Order Orthoptera. Families Oedishiidae (Brauckmann, 2007) and Thuringoedischiidae (Zessin, 1997).

Obora. Czech Republic, Blansko District, southern Moravia, several outcrops of the Obora locality; Lower Permian, basal Sakmarian Stage (lower Upper Rotliegend), middle member of Letovice Formation, Băcovian Horizon (Stamberg and Zajíc, 2008).

The checklist of insects is based on Stamberg and Zajíc (2008) and *Paleobiology Database* (2014), unless specified otherwise.

Order Odonata. Families Meganeuridae, Alectoneuridae, Engisopteridae, and Oboraneuridae.

Order Dictyoneurida. Families Arcioneuridae, Ancopteridae, Caulopteridae, Hanidae, Elmoboriidae, Homiopteridae, and Calvertiellidae.

Order Mischopterida. Families Bardohymenidae, Alectoneuridae, Engisopteridae, and Moravohymenidae.

Order Diaphanopterida. Families Elmoidae, Martynoviidae, and Asthenohymenidae.

Order Hypoperlida. Families Hypoperlidae (Rasnitsyn, unpublished data) and Ischnoneuridae (Rasnitsyn and Aristov, 2013).

Order Ephemerida. Families Jarmilidae, Oboriphlebiidae, and Protereismatidae.

Order Syntonopteridae. Family Syntonopteridae.

Order Psocida. Family Permopsocidae.

Order Caloneurida. Family Caloneuridae.

Order Jurinida. Family Jurinidae.

Table 1. Fossil records of insect families in the studied assemblages

Family	First appearance	Records in analyzed localities	Last appearance
Dasyleptidae	C ₃ st [1]	Carrizo Arroyo [2], Wellington [3], Kityak [4], Kaltan [5]	T ₂ ani [6]
Meganeuridae	C ₂ b [5]	Obora [7], Wellington [3], Koshelevka [8], Solikamsk [10], Soyana, Lodève [11], Kargala [9]	P ₃ sdv [9]
Calvertiellidae	C [10]	Carrizo [2], Asselian, Obora [7], Wellington [3], Soyana [10], Lodève [12]	P ₃ sdv [9]
Caloneuridae	C [10]	Carrizo Arroyo [2], Obora [7], Wellington [3], Koshelevka [8], Soyana, Tikhie Gory [2], Lodève [12], Kityak [4], Kaltan [5], Kargala, Chepanikha [9]	P ₃ sdv [9]
Ischnoneuridae	C [10]	Carrizo Arroyo [2], Obora [7], Wellington [3], Koshelevka [8], Solikamsk [4], Soyana, Tikhie Gory, Chepanikha [9]	P ₃ vt [9]
Archescytinidae	Carrizo [2]	Obora, Wellington, Koshelevka, Vorkuta, Solikamsk, Soyana, Tikhie Gory, Kaltan [13]	P ₃ vt [9]
Palaeomanteidae	C ₂ [2]	Carrizo Arroyo [2], Asselian [7, 15], Obora [7], Wellington [3], Koshelevka [8], Vorkuta [14], Solikamsk [4], Soyana, Tikhie Gory [2], Kityak [4], Kaltan [5], Chepanikha [9]	P ₃ sdv [9]
Protomeropidae	C ₂ [15]	Asselian, Obora [7], Koshelevka [8]	P ₃ vt [9]
Phyloblattidae	C ₂ [10]	Carrizo Arroyo [16], Asselian [7], Obora [7], Sakmarian [17], Wellington [3], Koshelevka [8], Vorkuta [14], Tikhie Gory, Kityak [4], Chepanikha, Kargala [9]	K ₁ apt [18]
Archimylacridae	C ₂ [10]	Asselian [7, 15], Sakmarian [17], Koshelevka [8], Vorkuta [14], Solikamsk [19], Soyana [4]	P ₃ chan [20]
Spiloblattinidae	C ₂ [10]	Asselian [7], Wellington [3], Vorkuta [14], Kityak [4], Kargala [9]	T _{2/3} [21]
Mylacridae	C ₂ [10]	Asselian, Obora [7], Chepanikha [9]	T ₃ [10]
Protoplattinidae	C ₃ [26=22]	Soyana [4]	T ₂ [4]
Liomopteridae	C ₃ [32=23]	Carrizo Arroyo [2] Obora, Wellington, Koshelevka, Vorkuta [25], Solikamsk [27], Soyana, Tikhie Gory, Lodève, Kityak, Kaltan, Kargala, Chepanikha [25]	P ₃ vt [25]
Cacurgidae	C ₂ [27]	Castle Hollow, Chekarda [27]	P ₃ sdv [27]
Protophasmatidae	C [27]	Asselian, Sakmarian [27]	P ₃ sdv [27]
Neraphidiidae	C ₃ [24]	Koshelevka [24]	P ₂ urzh [24]
Syntonopteridae	C ₃ [10]	Obora [7], Lodève [26].	P ₂ capit [27]
Oedischiidae	C ₃ [10]	Asselian [7], Leuchtenburge [28], Wellington, Koshelevka [29], Solikamsk [30], Soyana, Tikhie Gory [29], Lodève [12], Chepanikha [9]	Chepanikha [9]
Blattinopseidae	C ₃ [10]	Asselian [7, 15], Obora [7], Wellington [3], Koshelevka [8], Vorkuta [14], Solikamsk [4], Soyana, Tikhie Gory [10]	Tikhie Gory [10]
Ampelipteridae	C ₃ [10]	Koshelevka [8], Vorkuta [14], Soyana [10]	Soyana [10]
Sylvaphlebiidae	C ₃ [31, 32]	Obora, Wellington, Koshelevka [25], Solikamsk [4], Soyana [4, 26]	Soyana [25]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Idelinellidae	C ₂ [33]	Koshelevka [33], Soyana [27]	Soyana [27]
Epideigmatidae	C ₃ [34]	Obora, Koshelevka, Soyana [34]	Soyana [34]
Spilapteridae	C ₃ [10]	Carrizo Arroyo [2], Wellington [3], Koshelevka [8], Vorkuta [14]	Vorkuta [14]
Sphecopteridae	C ₃ [10]	Vorkuta [14]	Vorkuta [14]
Geraridae	C ₃ [35]	Vorkuta [35]	Vorkuta [35]
Poroblattinidae	C ₃ [10]	Carrizo Arroyo [16], Asselian [7]	Poryvaevskii Mine P ₁ kg [5]
Subioblattidae	C ₂ [10]	Obora [7], Wellington [3]	T ₂ [10]
Necmylacridae	C ₂ [10]	Asselian of China [36]	Poryvaevskii Mine P ₁ kg [5]
Paralogidae	C ₃ [37]	Wellington [3], Koshelevka [8]	Koshelevka [8]
Cheliphlebiidae	C ₂ [4]	Carrizo Arroyo, Obora [4], Koshelevka [4]	Koshelevka [4]
Cnemidolestidae	C ₂ [24]	Sakmarian [24]	Kedrovka [24]
Dictyoneuridae	C ₃ [10]	Carrizo Arroyo [2], Obora [7], Wellington [3]	Wellington [3]
Breyeriidae	C ₃ [10]	Sakmarian [17]	Sakmarian [17]
Diaphanopteridae	C ₃ [10]	Sakmarian [17]	Sakmarian [17]
Erasipteridae	C [10]	Sakmarian [17]	Sakmarian [17]
Spanioderidae	C [24]	Carrizo Arroyo [24]	Sakmarian [24]
Homoiopteridae	C [10]	Obora [7]	Obora [7]
Eugereonidae	C [10]	Asselian [39]	P ₁ ass [39]
Hapalopteridae	C [10]	Carrizo [2]	Carrizo [2]
Martynoviidae	C ₃ [10]	Carrizo Arroyo [2] Obora [7], Wellington [3], Lodève [12]	Lodève [12]
Asthenohymenidae	C ₃ [10]	Carrizo Arroyo [2], Obora [7], Wellington [3], Koshelevka [8]	Koshelevka [8]
Probnidae	Carrizo [2]	Wellington [3]	Wellington [3]
Hanidae	C [10]	Carrizo Arroyo [2], Obora [7]	Obora [7]
Thuringoedischidae	Carrizo [2]	Asselian [30=28]	P ₁ sakm [28]
Luseiidae	Carrizo [38=37]	Carrizo [38=37]	Carrizo [37]
Tshekardocoleidae	Asselian [14=39]	Asselian [14=39], Obora [8=9], Sakmarian [17], Wellington [39=38], Koshelevka [12], Soyana [9]	Soyana [10]
Camptoneuritidae	Obora [40]	Obora [40], Wellington, Solikamsk, Soyana, Tikhie Gory [40]	Tikhie Gory [40]
Bardohymenidae	Obora [7]	Obora [7] Wellington [3], Koshelevka [12]	Koshelevka [12]
Elmoberiidae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Elmoidae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Permopsocidae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Archelytridae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Blattelytridae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Protelytridae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]
Elytroneuridae	Obora [7]	Obora [7], Wellington [3]	Wellington [3]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Arcioneuridae	Obora [7]	Obora [7]	Obora [7]
Ancopteridae	Obora [7]	Obora [7]	Obora [7]
Caulopteridae	Obora [7]	Obora [7]	Obora [7]
Jarmilidae	Obora [7]	Obora [7]	Obora [7]
Oboriphlebiidae	Obora [7]	Obora [7]	Obora [7]
Alectoneuridae	Obora [7]	Obora [7]	Obora [7]
Engisopteridae	Obora [7]	Obora [7]	Obora [7]
Oboraneuridae	Obora [7]	Obora [7]	Obora [7]
Cymbopsidae	Obora [7]	Obora [7]	Obora [7]
Planelytridae	Obora [7]	Obora [7]	Obora [7]
Havlatiidae	Obora [7]	Obora [7]	Obora [7]
Moravocoleidae	Obora [7]	Obora [7]	Obora [7]
Oborocoleidae	Obora [7]	Obora [7]	Obora [7]
Perlapsocidae	Sakmarian [41]	Sakmarian [41]	Sakmarian [41]
Rigattopteridae	Sakmarian [17]	Sakmarian [17]	Sakmarian [17]
Proedischiidae	Sakmarian [17]	Sakmarian [17]	Sakmarian [17]
Sphecorydaloididae	Sakmarian [17]	Sakmarian [17]	Sakmarian [17]
Velziopteridae	Sakmarian [17]	Sakmarian [17]	Sakmarian [17]
Tococladidae	Wellington [3]	Wellington [3], Koshelevka [8], Lodève [12], Kargala [9]	Kargala [9]
Coleoscytoidea fam. nov.	Wellington [13]	Wellington, Chepanikha [13]	Chepanikha [13]
Euryptilonidae	Wellington [27]	Wellington [27], Koshelevka [8], Kaltan [5]	Kaltan [5]
Permoberothidae	Wellington [3]	Wellington [3], Kityak [4]	Kityak [4]
Parelmoidae	Wellington [3]	Wellington [3], Koshelevka [8], Lodève [42]	Lodève [42]
Permothemistidae	Wellington [3]	Wellington [3], Koshelevka [8], Soyana, Tikhie Gory [43]	Tikhie Gory [43]
Permopanorpidae	Wellington [3]	Wellington [3], Soyana [10]	Soyana [10]
Protembiidae	Wellington [44]	Wellington [44], Koshelevka, Soyana [44]	Soyana [44]
Sojanoraphidiidae	Wellington [25]	Wellington [25], Koshelevka, Soyana [25]	Soyana [25]
Prothymenidae	Wellington [3]	Wellington [3], Koshelevka [8], Soyana [4]	Soyana [4]
Apheloneuridae	Wellington [3]	Wellington [3], Koshelevka [8]	Koshelevka [8]
Biarmohymenidae	Wellington [3]	Wellington [3], Koshelevka [8]	Koshelevka [8]
Chelopteridae	Wellington [3]	Wellington [3]	Koshelevka [8]
Permorphidiidae	Wellington [3]	Wellington [3]	Wellington [3]
Heteroptilidae	Wellington [3]	Wellington [3]	Wellington [3]
Nugioneuridae	Wellington [3]	Wellington [3]	Wellington [3]
Anelcanidae	Wellington [3]	Wellington [3]	Wellington [3]
Telactinopterigidae	Wellington [43]	Wellington, Koshelevka [44]	Koshelevka [44]
Raaschiidae	Wellington [25]	Wellington [25]	Wellington [25]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Atactophlebiidae	Koshelevka [25]	Koshelevka [25], Soyana, Tikhie Gory [25], Kityak [4]	Kityak [4]
Vorkutiidae	Koshelevka [8]	Koshelevka [8], Vorkuta [14], Kaltan [5]	Kaltan [5]
Euremiscidae	Koshelevka [25]	Koshelevka [25], Soyana, Lodève [25]	Lodève [25]
Permopectinidae	Koshelevka [14]	Koshelevka [14], Vorkuta [14]	Tesh P ₁ kg [4]
Permaeschnidae	Koshelevka [45]	Koshelevka, Soyana, Tikhie Gory [45]	Tikhie Gory [45]
Tshekardocephalidae	Koshelevka [8]	Koshelevka [12], Soyana [46]	Soyana [46]
Pinideliidae	Koshelevka [25]	Koshelevka [25], Solikamsk [25], Soyana [4]	Soyana [4]
Eukulojidae	Koshelevka [8]	Koshelevka [12], Soyana [9]	Soyana [9]
Tillyardembiidae	Koshelevka [19]	Koshelevka, Solikamsk, Soyana [19]	Soyana [9]
Bardacoleidae	Koshelevka [8]	Koshelevka [12], Vorkuta [9]	Vorkuta [9]
Diathemidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Paruraliidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Perlopseidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Pseudelcanidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Adumbratîmîrphidaă	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Uraloptysmatidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Îiracopteridae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Asiuropidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Perielytridae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Permetatoridae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Tsheñalculidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Personidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Montanuraliidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Tshekarchiereidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Synomaloptilidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Palaeomantiscidae	Koshelevka [8]	Koshelevka [8]	Koshelevka [8]
Solikamptilonidae	Solikamsk [45]	Solikamsk, Soyana [45]	Soyana [45]
Archisialidae	Soyana [10]	Soyana [10]	Soyana [10]
Permocentropidae	Soyana [10]	Soyana [10]	Soyana [10]
Kulojidae	Soyana [10]	Soyana [10]	Soyana [10]
Palingeniopsidae	Soyana [10]	Soyana [10]	Soyana [10]
Permepallagidae	Soyana [10]	Soyana [10]	Soyana [10]
Ivapteridae	Soyana [25]	Soyana [25]	Soyana [25]
Pholidoptilidae	Tikhie Gory [45]	Tikhie Gory [45]	Tikhie Gory [45]
Aspidohymenidae	Tikhie Gory [45]	Tikhie Gory [45]	Tikhie Gory [45]
Saxonagrionidae	Lodève [47]	Lodève [47]	Lodève [47]
Lodeveiidae	Lodève [47]	Lodève [47]	Lodève [47]
Lapeyriidae	Lodève [47]	Lodève [47]	Lodève [47]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Permostridulidae	Lodève [12]	Lodève [12]	Lodève [12]
Raphoglidae	Lodève [12]	Lodève [12]	Lodève [12]
Alexrasnitsyniidae	Lodève [42]	Lodève [42]	Lodève [42]
Archoglossopteridae	Kaltan [5]	Kaltan [5]	Kaltan [5]
Aenigmatidiidae	Kaltan [5]	Kaltan [5]	Kaltan [5]
Kaltanoneuridae	Kaltan [5]	Kaltan [5]	Kaltan [5]
Callimokaltaniidae	Kaltan [5]	Kaltan [5]	Kaltan [5]
Archiprobnidae	Kaltan [5]	Kaltan [5]	Kaltan [5]
Kargalopteridae	Kargala [9]	Kargala [9]	Kargala [9]
Homoeodictyidae	Kargala [9]	Kargala [9]	Kargala [9]
Psocidiidae	Carrizo [2]	Wellington [3], Koshelevka [8], Soyana [10].	P ₃ vt [9]
Misthodotidae	Asselian [39]	Asselian [39], Wellington [3], Koshelevka [8], Solikamsk [48]	P ₃ sdv [9]
Permothemopsidae	Asselian [27]	Asselian [27], Vorkuta, Soyana, Tikhie Gory, Kityak [27]	P ₃ sdv [27]
Lemmatophoridae	Asselian [39]	Asselian [14=39], Obora, Wellington, Koshelevka, Vorkuta, Solikamsk, Soyana [25], Kityak, Kaltan [4], Chepanikha [9]	P ₃ vt [4]
Jurinidae	Obora [7]	Obora [7], Soyana, Tikhie Gory [4], Lodève [11], Kityak [4], Kaltan [5], Chepanikha [9]	J ₁ [9]
Permosialidae	Obora [7]	Obora [7], Koshelevka [12], Vorkuta [14], Solikamsk [4], Tikhie Gory [9], Kityak [49], Kaltan [5], Chepanikha [9]	J ₃ [10]
Microptysmatidae	Obora [9]	Obora [9], Koshelevka, Solikamsk, Soyana, Tikhie Gory, Kaltan, Chepanikha [9]	P ₃ vt [9]
Tshekardominidae	Obora [4]	Obora [4], Wellington, Koshelevka, Soyana [25], Kityak [4], Chepanikha [9]	P ₂ urzh [9]
Moravohymenidae	Obora [7]	Obora [7]	P ₃ sdv [9]
Protereismatidae	Obora [7]	Wellington [3], Soyana, Tikhie Gory [4]	P ₃ sdv [9]
Sylviodidae	Obora [4]	Obora [4], Koshelevka, Soyana [4]	T ₃ [4]
Skaliciidae	Obora [25]	Soyana, Prokopevsk, Kargala [25]	P ₃ sdv [9]
Hypoperlidae	Obora [4]	Obora [4], Koshelevka [8], Solikamsk [4], Soyana, Tikhie Gory, Kaltan [9]	P ₃ sdv [9]
Sylvabestiidae	Obora [24]	Obora [24], Wellington, Koshelevka, Vorkuta, Soyana, Kityak, Chepanikha [24]	P ₃ sdv [24]
Prosbolidae	Sakmarian [13]	Sakmarian [13], Soyana, Tikhie Gory, Kityak, Kaltan, Chepanikha [13]	P ₃ vt [9]
Pereboreiidae	Sakmarian [13]	Sakmarian [13], Kityak, Kaltan, Kargala, Chepanikha [13]	P ₂ urzh [9]
Permocupedidae	Sakmarian [17]	Sakmarian [17], Soyana, Tikhie Gory, Kityak [10], Kaltan, Kargala, Chepanikha [9]	T ₂ [6]
Permithonidae	Sakmarian [17]	Sakmarian [17], Koshelevka [8], Soyana, Tikhie Gory, Kaltan [10], Kargala [9],	P ₃ vt [9]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Permochoristidae	Sakmarian [17]	Sakmarian [17], Wellington [3], Koshelevka [8], Vorkuta [14], Solikamsk, Soyana, Tikhie Gory, Kityak [50], Kaltan [5], Kargala, Chepanikha [9]	J [10]
Prosbolopseidae	Sakmarian [13]	Sakmarian [13], Koshelevka [8], Vorkuta, Solikamsk, Soyana, Kityak, Kaltan [13]	P ₂ urzh [9]
Dysmorphoptilidae	Sakmarian [13]	Sakmarian [13], Soyana, Chepanikha [13]	J ₁ [52]
Permembidae	Wellington [46]	Wellington [46], Koshelevka, Solikamsk, Soyana [46]	P ₃ sdv [9]
Prygidae	Wellington [24]	Wellington [24]	P ₃ vt [9]
Psoropteridae	Wellington [19=24]	Wellington [24]	T ₂ [24]
Lophioneuridae	Wellington [3]	Wellington [3], Koshelevka [8], Solikamsk [4], Soyana [10], Kaltan [5]	K ₂ st [51]
Kennedyidae	Wellington [45, 47]	Wellington [45, 47], Koshelevka, Soyana, Tikhie Gory, Kityak [45, 47]	T ₃ [54]
Ditaxineuridae	Wellington [45, 47]	Wellington, Koshelevka, Soyana [45, 47]	P ₃ sdv [9]
Permecanidae	Wellington [29]	Wellington [29], Koshelevka, Soyana, Kityak [29], Chepanikha [9]	T ₂ [29]
Pruvostitidae	Wellington [29]	Wellington [29], Koshelevka, Soyana, Tikhie Gory, Kityak, Kaltan, Kargala [29]	P ₃ sdv [9]
Boreoscytidae	Koshelevka [8]	Koshelevka [8], Soyana [13]	P ₂ urzh [9]
Ingruidae	Koshelevka [8]	Koshelevka [8], Soyana, Kaltan, Chepanikha [13]	P ₃ vt [9]
Permolestidae	Koshelevka [45, 47]	Koshelevka [8], Soyana, Tikhie Gory, Lodève, Kityak, Kargala [45, 47]	P ₃ sdv [9]
Bakteniidae	Koshelevka [47]	Koshelevka [47]	T ₂ [47]
Voltzialestidae	Koshelevka [47]	Koshelevka [47]	T ₂ [47]
Scytohymenidae	Koshelevka [8]	Koshelevka [8]	P ₃ sdv [9]
Parasialidae	Koshelevka [8]	Koshelevka [8], Soyana [10]	P ₃ sdv [9]
Glosselytridae	Koshelevka [8]	Koshelevka [8], Soyana [10]	T ₃ [9]
Bardapteridae	Koshelevka [8]	Koshelevka [8], Soyana [27]	P ₃ sdv [27]
Soyanopteridae	Koshelevka [8]	Koshelevka [8], Soyana [27]	P ₃ sdv [27]
Megakhosaridae	Koshelevka [8]	Koshelevka [8], Vorkuta, Solikamsk, Soyana, Kityak, Kaltan, Kargala, Chepanikha [27]	T ₂ [27]
Tshekardoperlidae	Koshelevka [8]	Koshelevka [8]	P ₃ sdv [9]
Palaeonemouridae	Koshelevka [8]	Koshelevka [8], Vorkuta, Solikamsk, Kityak, Kaltan, Kargala, Chepanikha [9]	P ₂ urzh [9]
Ideliidae	Koshelevka [27]	Koshelevka, Vorkuta, Solikamsk, Soyana, Tikhie Gory, Kityak, Kaltan, Kargala [27]	T ₂ [27]
Scytinopteridae	Vorkuta [13]	Vorkuta, Soyana, Tikhie Gory, Kityak, Kaltan, Chepanikha [13]	K ₁ [9]
Coleoscytidae	Vorkuta [13]	Vorkuta, Soyana, Tikhie Gory, Kityak [13]	P ₂ urzh [9]
Geinitziidae	Vorkuta [4]	Vorkuta, Soyana, Kityak [4], Kaltan [25]	J ₃ [9]
Mesorthopteridae	Vorkuta [27]	Vorkuta, Soyana, Kaltan [27]	J ₂ [4]

Table 1. (Contd.)

Family	First appearance	Records in analyzed localities	Last appearance
Protopsyllidiidae	Solikamsk [13]	Solikamsk [13], Soyana [13]	K ₂ [9]
Xenopteridae	Soyana [4]	Soyana [4]	T ₃ [29]
Chaulioditidae	Soyana [4]	Soyana [4], Kityak [52=53], Kargala [4], Chepanikha [52=53]	T ₂ [6]
Blattogryllidae	Soyana [27]	Soyana [27]	J ₃ [27]
Permofulgoridae	Soyana [10]	Soyana [10]	P ₃ vt [9]
Rhombocoleidae	Kityak [9]	Kityak [9], Kaltan [5], Kargala, Chepanikha [9]	P ₃ vt [9]
Permophasmatidae	Kityak [4]	Kityak [4]	P ₃ sdv [9]
Asiocoleidae	Kaltan [10]	Kaltan [10], Chepanikha [9]	J ₂ [9]
Schizocoleidae	Kaltan [10]	Kaltan [10], Chepanikha [9]	J ₂ [9]
Kaltanidae	Kaltan [5]	Kaltan [5], Chepanikha [9]	P ₂ urzh [9]
Palaeoperlidae	Kaltan [5]	Kaltan [5], Kargala [9]	P ₃ sdv [9]
Surijokocixiidae	Kargala [9]	Kargala [9], Chepanikha [9]	T ₃ [52]
Serpentivenidae	Chepanikha [9]	Chepanikha [9]	T ₂ [52]
Taldycupedidae	Kargala [9]	Kargala [9]	T ₃ [9]

References: [1] Engel, 2009; [2] Rasnitsyn et al., 2004; [3] Beckemeyer (2000); [4] our unpublished data; [5] Rohdendorf et al. (1961); [6] Bashkuev et al. (2012); [7] Stamberg and Zajic (2008); [8] Aristov et al. (2013); [9] Aristov et al. (2013); [10] Rasnitsyn and Quicke (2002); [11] Nel et al. (2009); [12] Béthoux (2008); [13] D.E. Shcherbakov, pers. comm. (2014); [14] Rasnitsyn et al. (2005); [15] Nel et al. (2007); [16] Schneider et al. (2004); [17] Pinto and Adami-Rodrigues, 1999; [18] Vršanský (2008); [19] Vishnyakova (1965); [20] Lin (1978); [21] Vishnyakova (1998); [22] Béthoux et al. (2005); [23] Brauckmann and Willmann (1990); [24] Aristov (2014); [25] Aristov (2009); [26] Prokop and Nel (2011); [27] Garrouste et al. (2009); [28] Zessin (1997); [29] Gorochoy (1995); [30] A.V. Gorochoy, pers. comm.; [31] Béthoux and Nel (2010); [32] Aristov (2004); [33] Aristov and Rasnitsyn (2014); [34] Aristov (2011); [35] Gorochoy (2004); [36] Hong (1980); [37] Nel et al. (2012); [38] A.G. Ponomarenko, pers. comm. (2014); [39] Brauckmann (2007); [40] Aristov et al. (2010); [41] Pinto et al. (2000); [42] Prokop and Nel (2011); [43] Sinitshenkova (1980); [44] Aristov and Rasnitsyn (2011); [45] D.V. Vassilenko, pers. comm. (2014); [46] Aristov and Rasnitsyn (2008); [47] Nel et al. (2012); [48] Novokshonov et al. (2002); [49] Novokshonov and Zuzhova (2004); [50] Novokshonov (1997); [51] Vishnyakova (1981); [52] Shcherbakov (2000); [53] Aristov et al. (2009); [54] Pritykina (1981).

Order Hemiptera. Family Archescytinidae (Shcherbakov, 2000).

Order Palaeomanteida. Families Permosialidae (Rasnitsyn and Aristov, 2013) and Palaeomanteidae.

Order Coleoptera. Families Tshekardocoleidae, Oborocoleidae, and Moravocoleidae.

Order Blattinopseida. Family Blattinopseidae.

Order Trichoptera. Families Protomeropidae, and Microptysmatidae.

Order Eoblattida. Family Cheliphlebiidae (Aristov, unpublished data).

Order Blattida. Phylloblattidae, Mylacridae, and Subioblattidae.

Order Grylloblattida. Families Sylvioididae, Tshekardominidae (Aristov, unpublished data), Sylvaphlebiidae, Lemmatophoridae, Epideigmatidae, Liomopteridae, Skaliciidae, Camptoneuritidae, and Havlatiidae (Aristov, 2009).

Order Cnemidolestida. Family Sylvabestiidae (Aristov, 2014).

Order Forficulida. Families Archelytridae, Blatte-lytridae, Protelytridae, Elytroneuridae, and Plane-lytridae (Shcherbakov, 2002).

Ordinis incertis. Family Cymbopsidae.

Sakmarian and Artinskian deposits of South America. Sakmarian Stage (*Paleobiology Database*, 2014) of Brazil: Itararé Subgroup, Paraná Basin, Rio Grande do Sul State, Caçapava do Sul, Durasnal locality, Budó Formation; Santa Catarina State, Anitápolis municipality, Anitápolis locality, Anitápolis Formation; Taió municipality, Taió locality, Rio do Sul Formation; São Paulo State, Boituva municipality, Boituva locality, Boituva Formation; Monte Mor municipality, Monte Mor locality, Monte-Mor Formation; Paraná State, Teixeira Soaris municipality, Teixeira Soaris locality, Teixeira Soaris Formation. Sakmarian (*Paleobiology Database*, 2014) stage of Argentina: San Luis Province, San Antonio Department, Bajo de Váiz locality, Bajo de Váiz Formation of Paganso Basin; Chubut Province, Central Patagonian Basin, Betancur locality, Nueva Lubeca Formation; Piedra Shotle locality, Piedra Shotle Formation;

Table 2. Distribution of insect families in the studied assemblages: (x) presence, (+) presence at supposedly the same level, but outside this assemblage (not counted but included in distribution)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Dasyleptidae	x	x				x							x	x			x
Meganeuridae	x			x		x	x		x	x		x				x	x
Calvertiellidae	x	x	x	x		x				x		x					x
Caloneuridae	x	x		x		x	x			x	x	x	x	x		x	x
Ischnoneuridae	x	x		x		x	x		x	x	x				x		x
Archescytinidae	x	x		x		x	x	x	x	x	x			x			x
Palaeomanteidae	x	x	x	x		x	x	x	x	x	x		x	x	x		x
Protomeropidae	x		x	x			x										x
Phyloblattidae	x	x	x	x	x	x	x	x			x		x		x	x	x
Archimylacridae	x		x		x		x	x	x	x							x
Spiloblattinidae	x		x			x		x					x			x	x
Mylacridae	x		x	x											x		x
Protblattinidae	x									x							x
Liomopteridae	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x
Cacurgidae	x					+	x										x
Protophasmatidae	x		x		x												x
Neraphidiidae	x						x								+		
Syntonopteridae	x			x								x			+		
Oedischiidae	x		x	+		x	x		x	x	x	x			x		
Blattinopseidae	x		x	x		x	x	x	x	x	x						
Homalophlebiidae	x		+								x						
Ampelipteridae	x						x	x		x							
Sylvaphlebiidae	x			x		x	x		x	x							
Idelinellidae	x						x			x							
Epideigmatidae	x			x			x			x							
Spilapteridae	x	x				x	x	x									
Sphecopteridae	x							x									
Geraridae	x							x									
Poroblattinidae	x	x	x					+									
Necmylacridae	x							+									
Paralogidae	x					x	x										
Cheliphlebiidae	x	x		x			x										
Cnemidolestidae	x				x		+										
Dictyoneuridae	x	x		x		x											

Table 2. (Contd.)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Breyeriidae	x				x												
Diaphanopteridae	x				x												
Erasipteridae	x				x												
Spanioderidae	x	x			x												
Homoiopteridae	x			x													
Eugereonidae	x		x														
Haplopteridae	x	x															
Martynoviidae		x		x		x						x					
Asthenohymenidae		x		x		x	x										
Probnidae		x				x											
Hanidae		x		x													
Thuringoedischiidae		x	x	+													
Luseiidae		x															
Tshekardocoleidae			x	x	x	x	x			x							
Camptoneuritidae				x		x			x	x	x						
Bardohymenidae				x		x	x										
Elmaboriidae				x		x											
Elmoidae				x		x											
Permopsocidae				x		x											
Archelytridae				x		x											
Blattelytridae				x		x											
Protelytridae				x		x											
Elytroneuridae				x		x											
Arcioneuridae				x													
Ancopteridae				x													
Caulopteridae				x													
Jarmilidae				x													
Oboriphlebiida				x													
Alectoneuridae				x													
Engisopteridae				x													
Oboraneuridae				x													
Cymbopsidae				x													
Planelytridae				x													
Havlatiidae				x													

Table 2. (Contd.)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Moravocoleidae				x													
Oborocoleidae				x													
Perlapsocidae					x												
Rigattopteridae					x												
Proedischiidae					x												
Sphecerydaloididae					x												
Velziopteridae					x												
Tococladidae						x	x					x					x
Coleoscytoidea fam. nov.						x									x		
Euryptilonidae						x	x							x			
Permoberothidae						x							x				
Parelmoidae						x	x					x					
Permothemistidae						x	x			x	x						
Permopanorpidae						x				x							
Protembiidae						x	x			x							
Sojanoraphidiidae						x	x			x							
Protohymenidae						x	x			x							
Apheloneuridae						x	x										
Biarmohymenidae						x	x										
Chelopteridae						x	x										
Permorphidiidae						x											
Heteroptilidae						x											
Nugioneuridae						x											
Anelcanidae						x											
Telactinopterigidae						x											
Raaschiidae						x											
Atactophlebiidae							x			x	x		x				
Vorkutiidae							x	x					+				
Euremiscidae							x			x		x					
Permopectinidae							x	x			+						
Permaeschnidae							x			x	x						
Tshekarcephalidae							x			x							
Pinideliidae							x		x	x							
Eukulojidae							x			x							

Table 2. (Contd.)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Tillyardembiidae							x		x	x							
Bardacoleidae							x	x									
Diathemidae							x										
Paruraliidae							x										
Perlopseidae							x										
Pseudelcanidae							x										
Adumbratomorphidae							x										
Uraloptysmatidae							x										
Miracopteridae							x										
Asiuropidae							x										
Perielytridae							x										
Permetatoridae							x										
Tshecalculidae							x										
Personidae							x										
Montanuraliidae							x										
Tshekarchiereidae							x										
Synomaloptilidae							x										
Solikamptilonidae									x	x							
Archisialidae										x							
Permocentropidae										x							
Kulojidae										x							
Palingeniopsidae										x							
Permepallagidae										x							
Ivapteridae										x							
Pholidoptilidae											x						
Aspidohymenidae											x						
Saxonagrionidae												x					
Lodeveidae												x					
Lapeyriidae												x					
Permostridulidae												x					
Raphoglididae												x					
Alexrasnitsyniidae												x					
Archoglossopteridae														x			

Table 2. (Contd.)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Aenigmatidiidae														x			
Kaltanoneuridae														x			
Callimokaltaniidae														x			
Archiprobnidae														x			
Kargalopteridae																x	
Homoeodictyidae																x	
Psocidiidae		x				x	x			x							x
Misthodotidae			x			x	x		x								x
Permothemopsidae			x					x		x	x		x				x
Lemmatophoridae			x	x		x	x	x	x	x			x	x	x		x
Jurinidae				x						x	x	x	x	x	x		x
Permosialidae				x			x	x	x	x	x		x	x	x		x
Microptysmatidae				x			x		x	x	x			x	x		x
Tshekardominidae				x		x	x			x			x		x		x
Moravohymenidae				x													x
Protereismatidae				x		x				x	x						x
Sylviodidae				x			x			x							x
Skaliciidae				x						x				+		x	x
Hypoperlidae	?			x			x		x	x	x			x			x
Sylvabestiidae				x		x	x	x		x			x		x		x
Prosbolidae					x					x	x		x	x	x		x
Pereboriidae					x								x	x	x	x	x
Permocupedidae					x					x	x		x	x	x	x	x
Permithonidae					x		x			x	x			x		x	x
Permochoristidae					x	x	x	x	x	x	x		x	x	x	x	x
Prosbolopseidae					x		x	x	x	x			x	x			x
Dysmorphoptilidae					x					x					x		x
Permembiiidae						x	x		x	x							x
Prygidae						x											x
Psoropteridae						x											x
Lophioneuridae						x	x		x	x				x			x
Kennedyidae						x	x			x	x		x				x
Ditaxineuridae						x	x			x							x
Permelmcanidae						x	x			x			x		x		x

Table 2. (Contd.)

	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
Pruvostitidae						x	x			x	x		x	x		x	x
Boreoscytidae							x			x							x
Ingruidae							x			x				x	x		x
Permolestidae							x			x	x	x	x			x	x
Bakteniidae							x										x
Voltzialesidae							x										x
Scytohymenidae							x										x
Parasialidae							x			x							x
Glosselytridae							x			x							x
Bardapteridae							x			x							x
Soyanopteridae							x			x							x
Megakhosaridae							x	x	x	x			x	x	x	x	x
Tshekardoperlidae							x										x
Palaeonemouridae							x	x	x				x	x	x	x	x
Ideliidae							x	x	x	x	x		x	x		x	x
Scytinopteridae								x		x	x		x	x	x		x
Coleoscytidae								x		x	x		x				x
Geinitziidae								x		x			x	x			x
Mesorthopteridae								x		x				x			x
Protopsyllidiidae									x	x							x
Xenopteridae										x							x
Chaulioditidae										x			x		x	x	x
Blattogryllidae										x							x
Permofulgoridae										x							x
Rhombocoleidae													x	x	x	x	x
?Permophasmatidae													x				x
Asiocoleidae														x	x		x
Schizocoleidae														x	x		x
Kaltanidae														x	x		x
Palaeoperlidae														x		x	x
Surijokocixiidae															x	x	x
Serpentivenidae															x		x
Taldycupedidae																x	x

La Rioja Province, La Rioja locality, Malanzan Formation. Artinskian (*Paleobiology Database*, 2014) stage of Brazil, Irati Formation. Paraná Basin: Rio Grande do Sul State, Minas do Leão municipality, Minas do Leão locality; Passo de São Borja, São Gabriel; São Paulo State, Piracicaba municipality, Piracicaba locality. Artinskian Stage (*Paleobiology Database*, 2014) of Uruguay, Cerro Largo department, El Barón, Melo Formation (correlated with Irati Formation; Pinto et al., 2000).

The checklist of insects is based on Pinto and Adami-Rodrigues (1999), Würdig et al. (1999), and Martins-Neto et al. (2007), unless specified otherwise.

Order Odonata. Family Erasipteridae.

Order Dictyoneurida. Family Breyeriidae.

Order Mischopterida. Family Sphecorydaloididae.

Order Diaphanopterida. Families Diaphanopteridae and Velizopteridae.

Order Hemiptera. Families Prosbolopseidae, Prosbolidae, Pereboriidae, and Dysmorphoptilidae (D.E. Shcherbakov, pers. comm., 2014).

Order Coleoptera. Family Permocupedidae.

Order Neuroptera. Family Permithonidae

Order Mecoptera. Families Permochoristidae.

Order Eoblattida. Family Protophasmatidae (Aristov, unpublished data).

Order Cnemidolestida. Families Cnemidolestidae and Spanioderidae (Aristov, 2014).

Order Blattida. Families Phyloblattidae and Achimylacridae.

Ordinis incertis. Families Perlapsocidae (Pinto et al., 2000), Rigattopteridae, and Proedischiidae.

Wellington Formation, United States. Leonardian (basal Kungurian) Stage: Dickinson County, Elmo locality; Carlton Member, Oklahoma, Noble County; Midco locality (outcrops Billings, Perry, Tasch Noble, etc.); Midco Member (Beckermeyer and Hall, 2007).

The checklist of insects is based on Beckermeyer (2000) and *Paleobiology Database* (2014), unless specified otherwise.

Order Machilida. Family Dasyleptidae.

Order Ephemerida. Families Mithodotidae and Protereismatidae.

Order Odonata. Families Meganeuridae, Paralagidae, Kennedyidae, and Ditaxineuridae.

Order Blattinopseida. Family Blattinopseidae.

Order Caloneurida. Family Caloneuridae.

Order Hypoperlida. Families Ischnoneuridae (Rasnitsyn and Aristov, 2013), Tococladidae, Heteroptilidae, and Nugioneuridae.

Order Dictyoneurida. Families Calvertiellidae, Elmoboriidae, and Spilapteridae.

Order Mischopterida. Families Bardohymenidae, Protohymenidae, and Permothemistidae.

Order Diaphanopterida. Families Asthenohymenidae, Martynoviidae, Elmoidae, Parelmoidae, and Biarmohymenidae.

Order Psocida. Families Psocidiidae, and Permopsocidae.

Order Thripida. Family Lophioneuridae.

Order Hemiptera. Family Archescytinidae (D.E. Shcherbakov, pers. comm., 2014).

Order Palaeomanteida. Families Permembaliidae (Aristov and Rasnitsyn, 2008) and Palaeomanteidae.

Order Coleoptera. Family Tshekardocoleidae (A.G. Ponomarenko, pers. comm., 2014).

Order Jurinida. Family Permoberothidae.

Order Mecoptera. Families Permochoristidae and Permopanorpidae.

Order Eoblattida. Family Protelemiidae (Aristov and Rasnitsyn, 2011).

Order Blattida. Families Spiloblattinidae and Phyloblattidae.

Order Grylloblattida. Families Liomopteridae, Euryptilonidae, Lemmatophoridae, Sylvaphlebiidae, Probnidae, Chelopteridae, Raashiidae, Sojanoraphidiidae, Tshekardominidae (Aristov, 2009), Camptoneuritidae (Aristov et al., 2010), and Telactinopterigidae (Aristov and Rasnitsyn, 2011).

Order Cnemidolestida. Families Psoropteridae, Sylvabestiidae (Aristov, 2014), and Prygidae (Aristov and Rasnitsyn, 2014).

Order Forficulida. Families Archelytridae, Elytronuridae, Blattelytridae, and Protelytridae (Shcherbakov, 2002).

Order Orthoptera. Families Oedischiidae, Permellcanidae, Anelcanidae, Permographidiidae, and Pruvostitidae.

Ordinis incertis. Family Apheloneuridae.

Koshelevka Formation. Russia, Perm Region, Upper Kungurian Stage, Irenskian Horizon: Suksunskii District, Chekarda and Yulaevo localities; Kishertskii District, Barda locality (=Krasnaya Glinka, =Matveevo, =Krutaya Katushka); Kishert' locality (=Sylva I = Spas-Barda, =Zapolinskii Log, =Salamatinskii Log; Aristov, 2004).

The checklist of insects is based on Aristov et al. (2013).

Order Ephemerida. Family Mithodotidae.

Order Syntonopteridae. Family Iiracopteridae.

Order Odonata. Families Meganeuridae, Ditaxineuridae, Kennedyidae, Permolestidae, Permaeschnidae, Bakteniidae, Paralagidae, and Voltzialesidae.

Order Blattinopseida. Family Blattinopseidae.

Order Caloneurida. Families Caloneuridae and Tshecalculidae.

Order Hypoperlida. Families Hypoperlidae, Ischnoneuridae, Synomaloptilidae, Ampelipteridae, Perielytridae, Tococladidae, and Asiuripidae.

Order Dictyoneurida. Families Spilapteridae, Biarmohymenidae, and Eukulojidae.

Order Mischopterida. Families Protohymeniade, Bardohymenidae, Scytomyzidae, Vorkutiidae, Permothemistidae, and Diathemidae.

Order Diaphanopterida. Families Astenohymenidae, Parelmoidae, and Paruraliidae.

Order Psocida. Family Psocidiidae.

Order Thripida. Family Lophioneuridae.

Order Hemiptera. Families Archescytinidae, Boreoscytidae, Ingridae, Prosbolopseidae, and Coleoscytoidea fam. nov. (D.E. Shcherbakov, pers. comm., 2014).

Order Palaeomanteida. Families Palaeomanteidae, Permosialidae, Permembidae, and Palaeomantisidae.

Order Coleoptera. Family Tshekardocoleidae.

Order Megaloptera. Family Parasialidae.

Order Neuroptera. Family Permithonidae.

Order Jurinida. Family Glosselytridae.

Order Panorpida. Family Permochoristidae.

Order Trichoptera. Families Protomeropidae, Microptysmatidae, and Uraloptysmatidae.

Order Eoblattida. Families Cheliphlebiidae, Protembiidae, Idelinellidae, and Soyanopteridae.

Order Blattida. Families Phylloblattidae and Archimylacridae.

Order Cnemidolestida. Families Tillyardembidae, Sylvabestidae and Neraphidiidae.

Order Grylloblattida. Families Lemmatophoridae, Sylvaphlebiidae, Euremiscidae, Sylvioidae, Liomopteridae, Epideigmatidae, Cacurgidae, Ideliidae, Euryptilonidae, Megakhosaridae, Pinideliidae, Bardapteridae, Sojanoraphidiidae, Atactophlebiidae, Tshekardominidae, and Chelopteridae.

Order Perlida. Families Perlopseidae, Tshekardopelidae, and Palaeonemouridae.

Order Forficulida. Family Bardacoleidae.

Order Orthoptera. Families Oedischiidae, Pruvostitidae, Adumbratomorphidae, Pseudelcanidae, and Permcanidae.

Ordinis incertis. Families Personidae, Tshekarchiereidae, Montanuraliidae, Permetatoridae, Tshekarchephalidae, and Apheloneuridae.

Vorkuta. Russia, Perm Region, Pechora Coal Field, cores of boreholes in the Vorkuta River Basin; Lower Permian, Kungurian and Ufimian stages (Vodolazskaya et al., 2013), Vorkuta Group, Lek-Vorkuta and Inta formations.

The checklist of insects is mostly based on Rasnitsyn et al. (2005).

Order Blattinopseida. Family Blattinopseidae.

Order Hypoperlida. Family Ampelipteridae.

Order Dictyoneurida. Family Spilapteridae.

Order Mischopterida. Family Vorkutiidae.

Order Megasecoptera. Family Sphecopteridae.

Order Hemiptera. Families Archescytinidae, Prosbolopseidae, Scytinopteridae, and Coleoscytidae (D.E. Shcherbakov, pers. comm., 2014).

Order Palaeomanteida. Families Palaeomanteidae and Permosialidae.

Order Mecoptera. Family Permochoristidae.

Order Blattida. Families Phylloblattidae, Archimylacridae, and Spiloblattinidae.

Order Cnemidolestida. Family Sylvabestidae (Aristov, 2014).

Order Grylloblattida. Families Mesorthopteridae (Aristov, 2014), Geinitziidae, Megakhosaridae, Ideliidae, Permothermopsidae, Permopectinidae, Liomopteridae, and Lemmatophoridae.

Order Forficulida. Family Bardacoleidae.

Order Perlida. Family Palaeonemouridae.

Order Mesotitanida. Family Geraridae.

Solikamsk Formation. Russia, Perm Region; Lower Permian, Ufimian Stage, Upper Solikamsk Subformation: Solikamskii District, Tyul'kino locality (Aristov, 2010; Bashkuev, 2010); Cherdynskii District, Mogil'nikovo locality (Novokshonov et al., 2002); Moshevo locality (Zalesskii, 1948).

Order Ephemerida. Family Mithodotidae (Novokshonov et al., 2002).

Order Odonata. Families Meganeuridae (Novokshonov et al., 2002) and Solikamptilonidae (Zalesskii, 1948).

Order Blattinopseida. Family Blattinopseidae.

Order Hypoperlida. Families Hypoperlidae (Novokshonov et al., 2002) and Ishnoneuridae.

Order Tripida. Family Lophioneuridae.

Order Hemiptera. Families Archescytinidae, Prosbolopseidae, and Protosyllidiidae (D.E. Shcherbakov, pers. comm., 2014).

Order Palaeomanteida. Families Palaeomanteidae (Novokshonov et al., 2002), Permembidae (Aristov and Rasnitsyn, 2008), and Permosialidae.

Order Mecoptera. Family Permochoristidae (Bashkuev, 2010).

Order Trichoptera. Family Microptysmatidae (I.D. Sukacheva, pers. comm., 2014).

Order Cnemidolestida. Family Tillyardembidae (Aristov and Rasnitsyn, 2014).

Order Grylloblattida. Families Liomopteridae, Lemmatophoridae, Megakhosaridae, Ideliidae, Pinideliidae (Aristov, 2010), Camptoneuridae (Aristov et al., 2010), and Sylvaphlebiidae.

Order Perlida. Family Palaeonemouridae (N.D. Sinitschenkova, pers. comm., 2014).

Order Orthoptera. Family Oedischiidae (Gorochov, 1995).

Soyana. Russia, Arkhangelsk Region, Mezenskii District, Soyana locality (outcrops Soyana, Letopala, Iva-Gora, etc.); Middle Permian, Lower Kazanian Substage, Iva-Gora Beds. The checklist is based on Rasnitsyn and Quicke (2002), unless specified otherwise.

Order Ephemerida. Families Palingeniopsidae and Protereismatidae.

Order Odonata. Families Meganeuridae, Permaeschnidae, Ditaxineuridae, Permolestidae, Permepalagidae, Kennedyidae, and Solikamptilonidae (Nel et al., 2012; D.V. Vassilenko, pers. comm., 2014).

Order Blattinopseida. Family Blattinopseidae.

Order Caloneurida. Family Caloneuridae.

Order Hypoperlida. Families Hypoperlidae, Ischnoneuridae, and Ampelipteridae.

Order Dictyoneurida. Families Calvertiellidae and Eukulojidae.

Order Mischopterida. Families Permothemistidae and Protohymenidae.

Order Diaphanopterida. Family Kulojidae.

Order Tripida. Family Lophioneuridae.

Order Psocida. Family Psocidiidae.

Order Hemiptera. Families Archescytinidae, Prosbolidae, Boreoscytidae, Prosbolopseidae, Ingruidae, Scytinopteridae, Protopsyllidiidae, Dysmorphoptilidae, and Coleoscytidae (D.E. Shcherbakov, pers. comm., 2014).

Order Palaeomanteida. Families Palaeomanteidae, Permosialidae, and Permembidae.

Order Coleoptera. Families Tshekardocoleidae and Permocupedidae.

Order Mecoptera. Families Permochoristidae, Permopanorpidae, and Permocentropidae.

Order Trichoptera. Family Microptysmatidae.

Order Megaloptera. Families Parasialidae and Archisialidae.

Order Neuroptera. Family Permithonidae.

Order Jurinida. Families Jurinidae and Glosselytridae.

Order Eoblattida. Families Idelinellidae (Aristov and Rasnitsyn, 2014), Protembaliidae, and Sojanopteridae (Aristov and Rasnitsyn, 2011).

Order Blattida. Family Archimylacridae.

Order Gylloblattida. Families Chaulioditidae, Geintziidae, Lemmatophoridae, Liomopteridae, Epideigmatidae, Camptoneuritidae, Sylvaphlebiidae, Euremiscidae, Ivapteridae, Skaliciidae, Mesorthopteridae, Ideliidae, Permothermopsidae, Megakhosaridae, Blattogryllidae, Bardapteridae, Sylvioididae, Atactophlebiidae, Pinideliidae, Sojanoraphidiidae, Tshekardominidae, and Protoblattinidae (Aristov, 2009, 2014; unpublished data).

Order Cnemidolestida. Families Tillyardembiidae and Sylvestiidae (Aristov, 2014).

Order Forficulida. Family Permofulgoridae (Shcherbakov, 2002).

Order Orthoptera. Families Oedischiidae, Pruvostidae, Permelmcanidae, and Xenopteridae.

Ordinis incertis. Family Tshekarcephalidae (Aristov and Rasnitsyn, 2008).

Tikhie Gory. Russia, Tatarstan, Mendelevskii District, Tikhie Gory locality; Middle Permian, Lower Kazanian Substage, Baitugan Formation.

The checklist is based mostly on Golubev et al. (2007).

Order Ephemera. Family Prottereismatidae.

Order Odonata. Families Pholidoptilidae, Permolestidae, Permaeschnidae, and Kennedyidae (Nel et al., 2012; D.V. Vassilenko, pers. comm., 2014).

Order Hypoperlida. Families Hypoperlidae and Ischnoneuridae.

Order Mischopterida. Families Aspidohymenidae and Permothemistidae.

Order Blattinopseida. Family Blattinopseidae.

Order Caloneurida. Family Caloneuridae.

Order Jurinida. Family Jurinidae.

Order Hemiptera. Families Archescytinidae, Prosbolidae, Scytinopteridae, and Coleoscytidae (D.E. Shcherbakov, pers. comm., 2014).

Order Neuroptera. Family Permithonidae.

Order Coleoptera. Family Permocupedidae.

Order Palaeomanteida. Families Palaeomanteidae and Permosialidae.

Order Mecoptera. Family Permochoristidae.

Order Trichoptera. Family Microptysmatidae.

Order Blattida. Family Phylloblattidae.

Order Grylloblattida. Families Atactophlebiidae, Ideliidae, Permothermopsidae, Camptoneuritidae, and Liomopteridae.

Order Orthoptera. Families Oedischiidae and Pruvostidae.

Lodève. France, Hérault and Languedoc provinces, several localities (La Lieude farm, Les Canals, Arièges, Les Vignasses, etc.) in the Lodève Basin; Middle Permian, Roadian (Lower Kazanian) Stage (*Paleobiology Database*, 2014); Salagou Formation, Merifrons Member.

The checklist is based mostly on Béthoux (2008), unless specified otherwise.

Order Syntonopterida. Family Syntonopteridae (Prokop and Nel, 2011).

Order Odonata. Families Meganeuridae, Saxona-grionidae, Lodeveidae, Permolestidae, and Lapeyriidae (Nel et al., 2012; D.V. Vassilenko, pers. comm., 2014).

Order Hypoperlida. Family Tococladidae.

Order Dictyoneurida. Family Calvertiellidae.

Order Diaphanopterida. Families Parelmoidae, Alexrasnitsyniidae (Prokop and Nel, 2011), and Martynoviidae.

Order Caloneurida. Families Caloneuridae and Permostridulidae.

Order Jurinida. Family Jurinidae.

Order Grylloblattida. Families Euremiscidae and Liomopteridae (Aristov, 2009).

Order Orthoptera. Families Oedischiidae and Raphogliidae.

Kityak. Russia, Kirov Region, Malmyzhskii District, Kityak locality; Middle Permian, Upper Kaza-

nian Substage, Belebeevskii Formation (Shcherbakov, 2008).

The checklist is based mostly on Rasnitsyn and Quicke (2002) and on unpublished data of the authors.

Order Machilida. Family Dasyleptidae.

Order Odonata. Family Permolestidae and Kennedyidae (D.V. Vassilenko, pers. comm., 2014).

Order Caloneurida. Family Caloneuridae.

Order Hemiptera. Families Prosbolidae, Pereboriidae, Prosbolopseidae, Scytinopteridae and Coleoscytidae (D.E. Shcherbakov, pers. comm., 2014).

Order Coleoptera. Families Rhombocoleidae and Permocupedidae.

Order Palaeomanteida. Families Permosialidae and Palaeomanteidae.

Order Mecoptera. Family Permochoristidae.

Order Jurinida. Families Jurinidae and Permoberothidae.

Order Blattida. Families Spiloblattinidae and Phylloblattidae.

Order Grylloblattida. Families Chaulioditidae, Liomopteridae, Lemmatophoridae Megakhosaridae, Ideliidae, Permothrompsidae, Atactophlebiidae, Tshekardominidae, and Geinitziidae.

Order Cnemidolestida. Family Sylvabestiidae (Aristov, 2014).

Order Perlida. Family Palaeonemouridae.

Order Orthoptera. Families Permelmcanidae and Pruvostitidae.

Order Phasmatida. Family Permophasmatidae.

Kaltan and Sarbala. Russia, Kemerovo Region, Kuzedeevskii District; Middle Permian, Upper Kazanian Substage, Mitina Formation (Shcherbakov, 2008), Kaltan and Sarbala localities.

The checklist is based mostly on Rohdendorf et al. (1961) and Rasnitsyn and Quicke (2002).

Order Machilida. Family Dasyleptidae.

Order Odonata. Families Kaltanoneuridae and Callimokaltaniidae.

Order Hypoperlida. Family Hypoperlidae.

Order Diaphanopterida. Family Aenigmatidiidae.

Order Mischopterida. Family Vorkutiidae.

Order Jurinida. Families Jurinidae and Archoglossopteridae.

Order Caloneurida. Family Caloneuridae (Rasnitsyn et al., 2004).

Order Thripida. Family Lophioneuridae.

Order Hemiptera. Families Archescytinidae, Prosbolidae, Pereboriidae, Prosbolopseidae, Ingridae, and Scytinopteridae (D.E. Shcherbakov, pers. comm., 2014).

Order Coleoptera. Families Rhombocoleidae, Permocupedidae, Asiocoleidae, and Schizocoleidae.

Order Neuroptera. Family Permithonidae.

Order Palaeomanteida. Families Palaeomanteidae and Permosialidae.

Order Mecoptera. Families Kaltanidae and Permochoristidae.

Order Trichoptera. Family Microptysmatidae.

Order Grylloblattida. Families Lemmatophoridae (Aristov, unpublished data), Ideliidae, Euryptilonidae, Megakhosaridae, Liomopteridae, Archiprobnidae, Kortshakoliidae, and Geinitziidae (Aristov, 2009).

Order Perlida. Families Palaeoperlidae and Palaeonemouridae.

Order Orthoptera. Family Pruvostitidae (Gorochov, 1995).

Chepanikha and Kostovaty. Udmurtia, Zav'yalovskii and Votkinskii districts; Middle Permian, Urzhumian Stage (*Ulemosaurus svijagensis* Zone), Chepanikha and Kostovaty localities. The checklist is based on Aristov et al. (2013).

Order Hypoperlida. Family Ischnoneuridae.

Order Palaeomanteida. Families Palaeomanteidae and Permosialidae.

Order Hemiptera. Families Ingridae, Scytinopteridae, Pereboriidae, Surijokocixiidae, Serpentinidae, Prosbolidae, and Dysmorphoptilidae.

Order Jurinida. Family Jurinidae.

Order Coleoptera. Families Permocupedidae, Asiocoleidae, Rhombocoleidae, and Schizophoridae.

Order Panorpida. Families Permochoristidae and Kaltanidae.

Order Trichoptera. Family Microptysmatidae.

Order Blattida. Families Mylacridae and Phylloblattidae.

Order Grylloblattida. Families Chaulioditidae, Liomopteridae, Lemmatophoridae, Megakhosaridae, Tshekardominidae, and Permuliidae.

Order Perlida. Family Palaeonemouridae.

Order Orthoptera. Families Permelmcanidae and Oedischiidae.

Kargala. Orenburg Region, Sakmarskii District, Middle Permian, Urzhumian Stage, Amanak Formation (*Estemmenosuchus uralensis* zone), dump of Kargala Copper Mines. The checklist is based on Aristov et al. (2013).

Order Odonata. Families Permolestidae and Meganeuridae.

Order Caloneurida. Family Caloneuridae.

Order Hemiptera. Families Surijokocixiidae and Pereboridae.

Order Coleoptera. Families Rhombocoleidae, Permocupedidae, and Taldycupedidae.

Order Neuroptera. Family Permithonidae.

Order Panorpida. Family Permochoristidae.

Order Blattida. Families Phylloblattidae and Spiloblattinidae.

Order Grylloblattida. Families Liomopteridae, Megakhosaridae, Ideliidae, Skaliciidae, and Kargalopteridae.

Order Perlida. Families Palaeonemouridae and Palaeoperlidae.

Order Orthoptera. Family Pruvostitidae.

Insecta incertae sedis. Family Homoeodictyidae.

METHODS OF ANALYSIS

The data on faunas were analyzed using the methods described in detail previously (Rasnitsyn et al., 2013; Aristov et al., 2013); therefore, they are discussed here briefly. The primary data are the composition of insect families in particular localities or, in some cases, in groups of localities of supposedly approximately the same age and similar geographical position (for a lack of data on the Permian of Gondwana for the Sakmarian and Artinskian ages of Brazil and Argentina, we had to combine data more broadly, otherwise Gondwana would have been excluded from the analysis). The family taxonomic level is generally accepted as optimal for these purposes. Local fossil assemblages instead of complete faunas of sequential stratigraphic intervals are analyzed for reasons described in the above-cited publications. Organization of the analyzed assemblages into a linear sequence, which proved so problematic at the previous stage of this work, proved rather easy in this case (see below).

Tables 1 and 2 show the data on insect families represented in the assemblages studied. Table 3 shows the results of calculations of the following parameters of the assemblages analyzed:

(1) total number of insects recorded (often approximately estimated or even plausibly guessed, because a more or less precise sample size is rarely known);

(2) natural logarithm of this number, which is used in subsequent rows of the table to normalize respective values by the logarithm of the sample size; this is done in accordance with the conclusion of Pesenko (1982, p. 60) that such normalization is adequate, as confirmed by our previous results (Aristov et al., 2013) and results of the present study (see below); taking the logarithm additionally decreases the influence of the above-mentioned imprecision of the sample size estimates;

(3, 4) number of all families in each assemblage: (3) absolute and (4) normalized to sample size (4);

(5–7) number of first appearances of families (the earliest appearance of which in the fossil record is known from localities of this assemblage): (5) absolute, (6) normalized to sample size, and (7) relative (normalized to the number of families in assemblage);

(8–10) the same for the last (latest known) appearances of families, respectively;

(11) ratio of the numbers of first and last appearances (measure of the directedness of changes in diversity: the changes are positive if (11) > 1 or negative if (11) < 1);

(12) sum of first and last appearances of families normalized to the total number of families (*relative faunal turnover*, a measure of the rate of changes in diversity);

(13) sum of the first and last appearances of families normalized to the sample size (*normalized faunal turnover*, an alternative measure of the rate of changes in diversity);

(14, 15) number (absolute and normalized) of transitional families, i.e., families that appeared in the Carboniferous and survived at least until the Late Permian;

(16, 17) the same for families that appeared in the Carboniferous and did not survive until the Middle Permian (“the most ancient” families);

(18, 19) the same for families that appeared in the Carboniferous and survived until the Middle Permian, but disappeared later;

(20, 21) the same for families that appeared and became extinct in the Early Permian (Early Permian endemics);

(22, 23) the same for families that appeared in the Early Permian and survived until the Middle Permian, but disappeared later (endemic to the Early–Middle Permian);

(24, 25) the same for families that appeared and became extinct in the Middle Permian (endemic to the Middle Permian);

(26, 27) the same for all families that did not survive until the Late Permian (“ancient” families);

(28, 29) the same for all families that appeared no earlier than the Early Permian (“young” families);

(30, 31) the same for all families that appeared in the Middle Permian (“the youngest” families);

(32) ratio of the numbers of “ancient” families (that did not survive until the Late Permian) and “young” families (that appeared no earlier than the Early Permian).

In addition to the above-listed parameters shown in Table 3, we tested again the method developed by D.A. Rasnitsyn for optimizing the linear sequences by the minimum sum of gaps in the fossil record (Rasnitsyn et al., 2013; Aristov et al., 2013). It is known that stratigraphic sequences of localities and their assemblages are sometimes not reliably justified and often require testing and correcting. We have shown that the ratio of the number of “ancient” and “young” taxa in assemblages can be a very useful tool for such correcting. We also developed an additional tool of the above-mentioned method for optimizing sequences by the sum of ghost ranges, based on determining the sequences with the minimum sum of such ranges using exhaustive computer search through random sequences. A sequence is considered to be optimal if it includes the minimum total number of occasions in which each family has not been recorded within its known geological range (for details, see publications cited above). The results of applying this method to our material are shown in Tables 4 and 5. In our previ-

Table 3. Parameters of taxonomic diversity of the studied assemblages

	Parameter	Earlier	1 Carrizo Arroyo	2 Asselian of Middle Europe	3 Obora	4 Sakmarian, Artinskian of South America	5 Wellington Fm., Lower Kungurian	6 Koshelevka Fm., Upper Kungurian	7 Vorkuta	8 Solikamsk Fm., Ufimian	9 Soyana, Lower Kazanian	10 Tikhie Gory, Lower Kazanian	11 Lodève	12 Kityak, Upper Kazanian	13 Kaltan, Sarbala	14 Chepanikha, Kostovaty	15 Kargala	Later
1	Total number of specimens		200	1000	3000	500	23000	7000	560	600	6000	300	300	700	2300	400	300	
2	$\ln_{\text{total}}$		5.3	6.9	8.0	6.2	10.0	8.9	6.3	6.4	8.7	5.7	5.7	6.6	7.7	6.0	5.7	
3	Total number of families	41	21	17	54	21	63	90	27	26	78	31	18	32	36	23	29	
4	Families/ $\ln_{\text{total}}$		4.0	2.5	6.8	3.4	6.3	10.1	4.3	4.1	9.0	5.4	3.2	4.8	4.7	3.8	5.1	
5	Number of first appearances		7	4	32	12	27	39	4	2	10	2	6	2	9	2	3	
6	First/ $\ln_{\text{total}}$		1.3	0.6	4.0	1.9	2.7	4.4	0.6	0.3	1.2	0.4	1.1	0.3	1.2	0.3	0.5	
7	First/families		0.33	0.24	0.59	0.57	0.43	0.43	0.15	0.08	0.13	0.06	0.33	0.06	0.25	0.09	0.1	
8	Number of last appearances		2	1	15	9	15	22	4	0	20	7	9	2	6	2	3	
9	Last/ $\ln_{\text{total}}$		0.4	0.1	1.9	1.5	1.5	2.5	0.6	0	2.3	1.2	1.6	0.3	0.8	0.3	0.5	
10	Last/families		.10	.06	.28	.43	.24	.24	.15	0	.26	.23	.5	.06	.17	.09	.1	
11	First/last		3.5	4.0	2.1	1.3	1.8	1.8	1.0	0	0.5	0.3	0.7	1.0	1.5	1.0	1.0	
12	(First + last)/ $\ln_{\text{total}}$		1.7	0.7	6.8	3.4	4.2	6.9	1.3	0.3	3.4	1.6	1.7	0.6	1.9	0.7	1.1	
13	(First + last)/families		0.4	0.3	0.9	1.0	0.7	0.7	0.3	0.1	0.4	0.3	0.8	0.1	0.4	0.2	0.2	
14	Transitional		8	8	10	3	10	10	6	6	9	6	4	6	5	5	5	
15	Transitional/ $\ln_{\text{total}}$		1.5	1.2	1.3	0.5	1.0	1.1	1.4	0.9	1.0	1.1	0.7	0.9	0.6	0.8	0.9	
16	C-P ₁		9	2	7	5	3	3	3	0	0	0	0	0	0	0	0	
17	(C-P ₁)/ $\ln_{\text{total}}$		1.7	0.3	0.9	0.8	0.3	0.3	0.5	0	0	0	0	0	0	0	0	
18	C-P ₂		0	2	6	0	3	7	2	3	6	3	3	0	0	1	0	
19	(C-P ₂)/ $\ln_{\text{total}}$		0	0.3	0.8	0	0.3	0.8	0.3	0.5	0.7	0.5	0.5	0	0	0.2	0	
20	P ₁		5	2	23	5	18	21	1	0	0	0	0	0	0	0	0	
21	(P ₁)/ $\ln_{\text{total}}$		0.9	0.3	2.9	0.8	1.8	2.4	0.2	0	0	0	0	0	0	0	0	
22	P ₁ -P ₂		1	1	3	1	13	17	2	4	15	4	3	2	1	1	1	
23	(P ₁ -P ₂)/ $\ln_{\text{total}}$		0.2	0.1	0.4	0.2	1.3	1.9	0.3	0.6	1.7	0.7	0.5	0.3	0.1	0.2	0.2	
24	P ₂		0	0	0	0	0	0	0	0	6	2	6	0	4	0	2	
25	(P ₂)/ $\ln_{\text{total}}$		0	0	0	0	0	0	0	0	0.7	0.4	1.1	0	0.5	0	0.4	
26	Pre-P ₃		12	6	33	11	38	48	8	7	27	9	12	2	6	2	3	
27	Pre-P ₃ / $\ln_{\text{total}}$		2.3	0.9	4.1	1.8	3.8	5.4	1.3	1.1	3.1	1.6	2.1	0.3	0.8	0.3	0.5	
28	Post-C		7	5	37	13	47	70	16	17	63	22	9	26	31	24	18	
29	Post-C/ $\ln_{\text{total}}$		1.3	0.7	4.6	2.1	4.7	7.9	0	2.7	7.2	3.9	1.6	3.9	4.0	4.0	3.2	
30	Post-P ₁		0	0	0	0	0	0	0	0	48	18	8	24	30	23	17	
31	(Post-P ₁)/ $\ln_{\text{total}}$		0	0	0	0	0	0	0	0	5.5	3.2	1.4	3.6	4.0	3.8	3.0	
32	Pre-P ₃ /post-C		1.7	1.2	0.9	0.8	0.8	0.7	0.5	0.4	0.4	0.4	1.3	0.1	0.2	0.1	0.2	

Table 4. Rearrangements, Kityak and Kaltan assemblages excluded: first column is sum of gaps; (Car) Carrizo Arroyo, (Ass) Asselian of Middle Europe, (Ob) Obora, (SA) Sakmarian and Artinskian of Argentina and Brazil, (Elm) Wellington Fm., (Chk) Koshelevka Fm., (Vr) Vorkuta, (Uf) Solikamsk Fm., (Soy) Soyana, (TGr) Tikhie Gory, (Ldv) Lodève, (Chp) Chepanikha and Kostovaty, (Kg) Kargala

554	Car	Ass	Ob	SA	Elm	Chk	Vr	Uf	Soy	TGr	Ldv	Chp	Kg
482	Ass	Car	SA	Ldv	Vr	TGr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
483	SA	Ass	Car	Ldv	Vr	TGr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
484	SA	Ass	Car	Ldv	TGr	Vr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
488	SA	Ass	Ldv	Car	Vr	TGr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
489	SA	Ass	Ldv	Car	TGr	Vr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
491	Ldv	Ass	Car	SA	Vr	TGr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
492	Ldv	Ass	Car	SA	TGr	Vr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
493	Ldv	SA	Ass	Car	Vr	TGr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
494	Ldv	SA	Ass	Car	TGr	Vr	Ob	Elm	Chk	Soy	Uf	Chp	Kg
498	Ldv	SA	Ass	Car	TGr	Ob	Vr	Elm	Chk	Soy	Uf	Chp	Kg

Table 5. Rearrangements, Lodève and Tikhie Gory assemblages excluded: (Kit) Kityak, (Klt) Kaltan and Sarbala, other designations as in Table 4

530	Car	Ass	Obo	SA	Elm	Chk	Vor	Ufa	Soy	Kit	Klt	Chp	Krg
490	Ass	Car	SA	Vor	Ufa	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt
491	SA	Ass	Car	Vor	Ufa	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt
493	SA	Ass	Car	Ufa	Vor	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt
496	SA	Ass	Car	Ufa	Vor	Obo	Elm	Chk	Soy	Krg	Kit	Chp	Klt
499	SA	Ass	Car	Ufa	Vor	Obo	Elm	Chk	Soy	Krg	Chp	Klt	Kit
500	SA	Ass	Vor	Car	Ufa	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt
503	SA	Ass	Vor	Car	Ufa	Obo	Elm	Chk	Soy	Krg	Kit	Chp	Klt
504	SA	Ass	Ufa	Car	Vor	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt
507	SA	Ass	Ufa	Car	Vor	Obo	Elm	Chk	Soy	Krg	Kit	Chp	Klt
509	SA	Vor	Ass	Car	Ufa	Obo	Elm	Chk	Soy	Kit	Krg	Chp	Klt

ous study, this method was on the whole less efficient than using the numbers of “ancient” and “young” taxa, but in some cases quite useful. We tried to use both methods again in this study and compare the results. Since the power of the available equipment, as in the previous case, allowed us to calculate the data for no more than 13 assemblages, our calculations covered two variants of sequences. In the first variant (Table 4), we excluded the assemblages of Kaltan and Kityak, the position of which in the temporal sequence raises no serious doubts. In the second variant (Table 5), we excluded the Lodève assemblage, which is most problematic in position in the sequence of assemblages (see below), and the Tikhie Gory assemblage, which is undoubtedly correlated stratigraphically with the more representative Soyana assemblage. It is expected that these results taken together provide sufficient notion about the optimal sequence of all assemblages studied by this method.

RESULTS

The results are combined in Figs. 1–6 and Tables 3–5. The parameter of the evolutionary aspect (level) of the fauna, which reflects the proportion of geologically more “ancient” and “younger” families (Fig. 1, fine line; Table 3, row 32), in general agrees with the accepted stratigraphic sequence of assemblages. It points to rapid “rejuvenation” of the family composition of assemblages from the Asselian (Carrizo Arroyo and Asselian of central Europe) to Sakmarian (Obora), followed by very smooth, almost invisible “rejuvenation” by the Late Kungurian of Chekarda and transition to the next more or less stable Ufimian—Early Kazanian level, followed in turn by the next, “youngest” Late Kazanian—Urzhumian level. The Lodève assemblage, correlated with the Kazanian Stage but corresponding according to the ratio of geologically “ancient” and “young” families rather to the Asselian level, sharply stands out of this sequence.

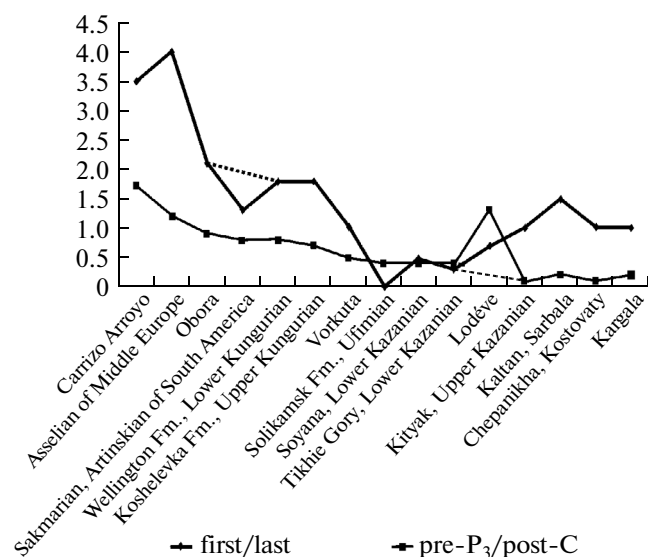


Fig. 1. Dynamics of directedness of changes (ratio of first and last appearances of families, bold line) in sequential insect assemblages of the Early and Middle Permian and evolutionary aspect of these assemblages (ratio of the number of geologically older and younger families). For more detail, see the text.

However, the problem here is most probably accounted for by the specificity of data processing in the material from Lodève rather than by dating or imperfection of the method. Six (which is on the whole very few) of 18 families of this assemblage are the first appearances and nine are the last appearances. This shows that the material was by no means evenly processed and only the most interesting records were selected for description, the most “ancient” and “youngest” in each group or simply unique finds. Therefore, the Lodève assemblage can by no means be viewed as adequately reflecting the composition of the fauna. If we exclude Lodève (dashed line), three visible boundaries of faunal “rejuvenation” can be distinguished within the studied interval: the Asselian–Sakmarian, Kungurian–Ufimian, and Early–Late Kazanian. This is confirmed by our previous conclusion that the parameter of the aspect of the fauna is an efficient tool of analysis (Aristov et al., 2013; Rasnitsyn et al., 2013).

The parameter of the directedness of changes in diversity (ratio of the number of first and last appearances of families in each of the studied assemblages; Fig. 1, bold line; Table 3, row 11) changes more intricately, but some trends become visible if we ignore the deviating data on the insufficiently representative (containing only 17 families) assemblage of South America (dashed line). Highly positive changes (strong dominance of first appearances of families), typical of the very basal Permian (Asselian), were later (Artinskian–Kungurian) replaced by stabilization at a moderate level and followed by a sharp fall in the

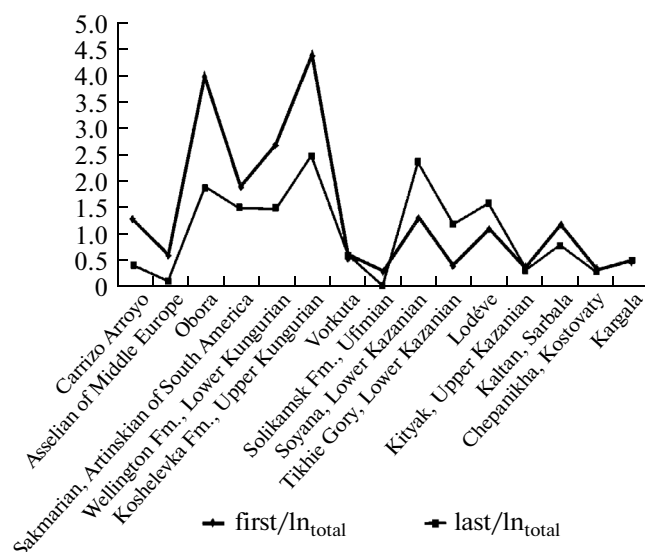


Fig. 2. Dynamics of normalized number of first and last appearances of insect families in sequential assemblages of the Early and Middle Permian. For more detail, see the text.

Ufimian and Early Kazanian down to the parity between the first and last records and even lower. In the Late Kazanian and Urzhumian, this parameter increases again and fluctuates around the balanced level. The fall of this parameter to zero at the Solikamsk level should not be taken for a special event, since the numbers of the first and last appearances are very scanty in this assemblage (zero and two, respectively) and, therefore, the particular value of the parameter cannot be considered reliable. On the whole, this parameter reveals the same three boundaries as in the above case and, hence, four characteristic intervals: the Asselian (highly positive changes), Artinskian and Kungurian (moderately positive changes), Ufimian–Early Kazanian (mostly negative), and Late Kazanian–Urzhumian (approximately neutral). As can be seen, the efficiency of this parameter is confirmed again.

An unexpected result of our previous study was the fact that a considerable fall in insect diversity in the terminal Permian resulted from decelerated diversification rather than extinction in the Vyatkian Time (Rasnitsyn, 2012; Aristov et al., 2013; Rasnitsyn et al., 2013). In the present study, such a strong fall (insect diversity crisis) is not revealed. Nevertheless, the numbers of the first and last appearances, both normalized by logarithm (Fig. 2) and relative (normalized by the number of families in the assemblage; Fig. 3), show the same effect. Certainly, the dominance of last appearances (fine line in Figs. 2 and 3) over first appearances (bold line) of families in the Early Kazanian is determined by the clearly low level of first appearances,

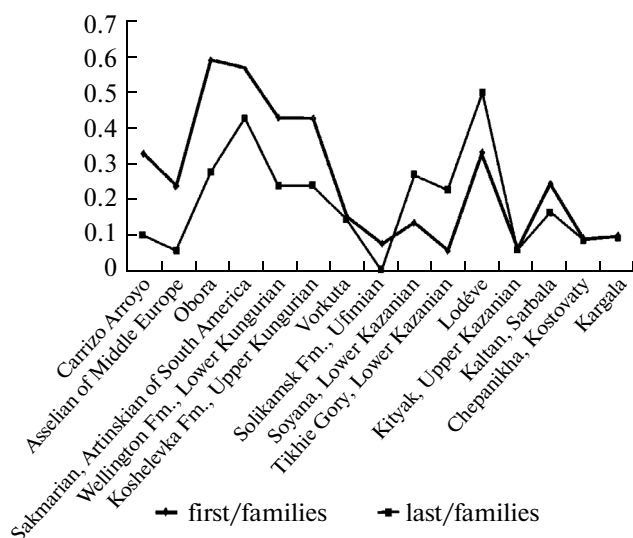


Fig. 3. Dynamics of the relative number of first and last records of insect families in sequential assemblages of the Early and Middle Permian. For more detail, see the text.

while the level of last appearances fluctuates on the whole within the same range as earlier. Meaningful interpretation of this phenomenon remains difficult, because it seems that serious biotic event associated with this interval has not yet been found. However, demonstration of the fact that selective deceleration of diversification is not a unique event in the evolution of organisms appears important. A possible mechanism of this deceleration was discussed by Rasnitsyn (2012).

The data on the dynamics of taxonomic diversity of insects irrespective of direction (Fig. 4; Table 3, rows 4, 12, 13), namely the normalized number of families (bold line in Fig. 4) and sum of the numbers of first and last appearances normalized by two different methods, by the sample size (by logarithm of the number of studied fossils: normalized faunal turnover; fine line) and by the number of families in each assemblage (relative faunal turnover; dashed line), are also very interesting. The first two parameters yielded two almost parallel, seemingly chaotically oscillating curves, similar to those obtained in our previous study. In both cases, the most dramatic peaks and dips correspond to larger and poorer samples, respectively, although the correlation is very imperfect: the highest peaks are yielded by the Koshchelevka assemblage, represented by a sample the size of which is only one-third of the size of the sample representing the much less diverse Wellington Formation. The size of the sample representing Kaltan is many times as great as the size of the samples representing Kityak and Kargala, but the levels of diversity known in these assemblages are comparable.

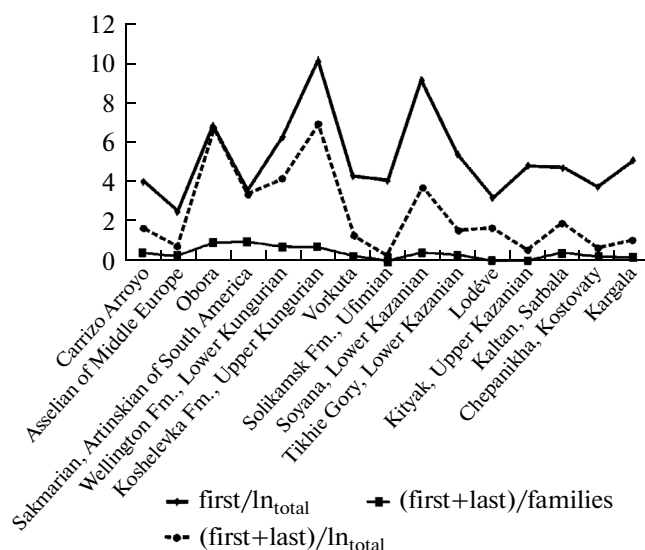


Fig. 4. Dynamics of the taxonomic diversity in sequential assemblages of the Early and Middle Permian: normalized number of families (bold line), normalized sum of the first and last appearances of families (dashed line), and relative sum of the first and last appearances of families (thin line). For more detail, see the text.

The fact that the two curves in question are parallel shows strong dependence of the rate of changes in diversity on the already reached level of diversity, as we noted previously (Aristov et al., 2013; Rasnitsyn et al., 2013). However, this dependence is clearly incomplete and, in order to reveal it, we used an additional parameter, the relative faunal turnover (the sum of the numbers of first and last appearances normalized by the number of insect families in the assemblage; Fig. 4, fine line; Table 3, row 13). The dependence revealed shows only two distinct boundaries and three characteristic intervals rather than three and four, respectively, as in the cases analyzed earlier. However, the general pattern remains the same, since both boundaries in this curve coincide with the first two boundaries in the earlier curves. In particular, the Asselian and Sakmarian–Kungurian intervals coincide, and the third, Ufimian–Urzhumian interval, is characterized by a low level of relative faunal turnover, i.e., the dependence of the intensity of changes on the reached level of diversity is almost exhaustive. In contrast, in the Sakmarian–Kungurian interval, the values of relative turnover are rather high, indicating clear influence of some additional factor.

The nature of this factor is yet to be revealed, but it is already obvious that, first, the quantitative parameters of dynamics of taxonomic diversity are efficient and should be used and studied further and, second, these parameters reveal nontrivial stepwise changes in the Early and Middle Permian history of insects. In particular, they indicate a brief Asselian period of intense diversification (many first appearances of fam-

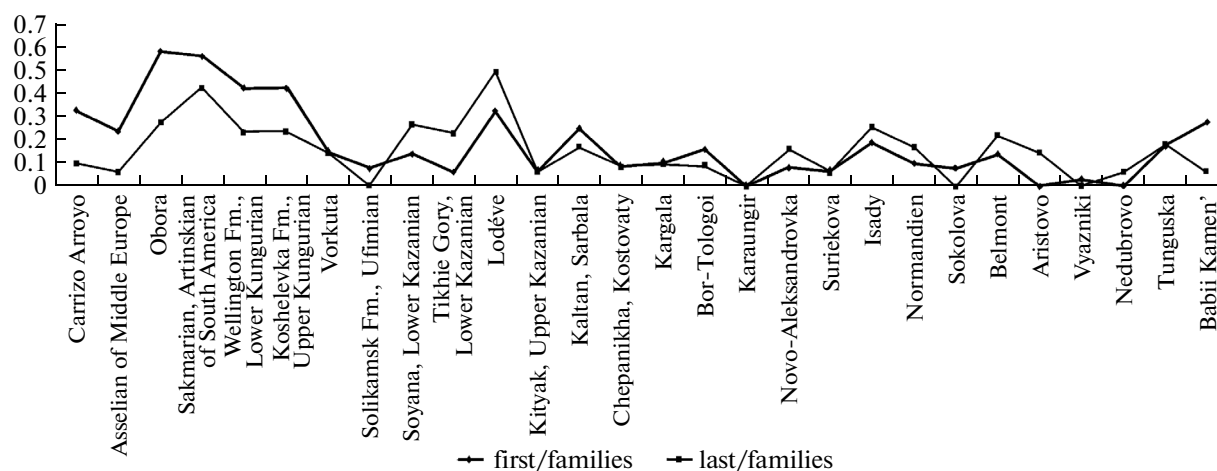


Fig. 5. Dynamics of total number of first (bold line) and last (fine line) records of families during the entire Permian. For more detail, see the text.

ilies) in combination with strong dependence of changes in diversity on the already reached level of diversity. This period is followed by the longer Sakmarian–Kungurian stage of moderately polarized (positive) changes in combination with considerable relative growth of diversity, which is less dependent on the reached level. This stage, in turn, is replaced by the Ufimian–Early Kazanian stage of changes in diversity (dominance of extinction) in combination with high dependence of changes in diversity on the reached level. The last parameter retains its level until the terminal Urzhumian, but beginning from the Late Kazanian, the direction of changes alters again, oscillating around the neutral level, slightly shifting towards the positive during the Kaltan Time. Furthermore, at each of the three recognized boundaries, assemblages become “rejuvenated” more visibly compared with changes within the adjacent stages. Therefore, the dynamics of transformation of the entomofauna in the Early and Middle Permian does not coincide with the stepwise development of those organisms the dynamics of which can be used for stratigraphic division of the Permian. Well-pronounced changes at the Kungurian–Ufimian boundary are especially important because of the widespread idea that the recognition of the Ufimian Stage is unjustified (for review, see Lozovskii et al., 2009; see also Gradstein et al., 2012, p. 663).

The method of rearrangements (Tables 4–5) this time yielded rather unconvincing results. Namely, the sequence of the most representative assemblages, Obora–Elmo–Chekarda–Soyana, is correctly and stably reproduced in both variants of the calculations. The assemblages of Carrizo Arroyo, the Asselian of Central Europe, Sakmarian and Artinskian of Argentina and Brazil, on the one hand, and Kityak, Chepanikha, and Kargala, on the other hand, are reproduced equally stably as situated earlier and later, respectively, than the above-listed group, but in different orders.

The position of remaining assemblages, i.e., Vorkuta, the Solikamsk Formation, Lodève, Tikhie Gory, and Kaltan, is not only variable but also paradoxical. Vorkuta, Lodève, and Tikhie Gory are constantly placed before the undoubtedly earlier Obora; Kaltan is constantly placed after the undoubtedly later Chepanikha and Kargala; and the Solikamsk Formation is placed either before Obora (in the first variant of rearrangements) or after Soyana (in the second variant). This means that the method of minimizing stratigraphic gaps is sensitive not only to random variations in distribution over the fossil record, but also to other factors, as clearly evidenced by the stably correct reproduction of the sequence of the most representative assemblages. Consistent but still unexplained behavior of other assemblages, some of which are rather rich (such as Tikhie Gory or Kaltan), is indicative of a considerable role played by some other regulatory parameters. Revealing these parameters is an interesting problem, which, however, is beyond the scope of this study.

We tried to put our results into broader context by combining some of them with those obtained earlier (Aristov et al., 2013) for the next interval of the Permian (Figs. 5, 6). The combined curves underline the above-noted peculiar features of the Paleozoic dynamics of insect diversity. It is confirmed that the level of extinction remained relatively stable during the entire Permian (especially if we disregard the data available on the problematic assemblages of Lodève and the Sakmarian–Artinskian of South America). A decrease in the rate of diversification at the terminal Early Permian and subsequent slow decrease in total diversity until the end of the period are clearly visible. The relatively high level of the general dynamics of diversity during most of the Early Permian is followed by stabilization of diversity at a considerably lower level during the entire Middle and Late Permian.

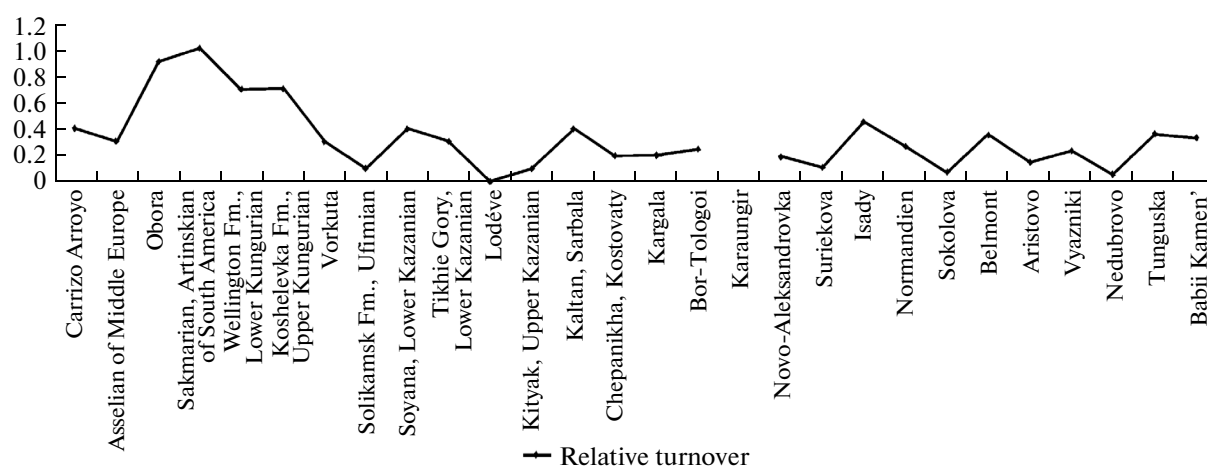


Fig. 6. Dynamics of relative faunal turnover throughout the Permian. For more detail, see the text.

CONCLUSIONS

The present study has confirmed on new material the adequacy to the task and promise of the approach developed by us for analyzing the dynamics of the taxonomic diversity of insects. In particular, we have largely confirmed that the dynamics of the evolutionary aspect of faunas matches the stratigraphic sequence of assemblages and revealed the stepwise character of the dynamics of diversity and coincidence of boundaries between the steps revealed using different parameters. It should be noted separately that we have confirmed the nontrivial mechanism of a decrease in diversity, which was first revealed in our previous study and represented by deceleration of diversification in combination with unchanged rate of extinction (Rasnitsyn, 2012; Aristov et al., 2013; Rasnitsyn, et al., 2013). In other words, biodiversity crises can manifest themselves in deceleration of evolution rather than in mass extinction of organisms. Thus, deceleration of diversification plays here the role of an independent (endogenous) factor of the biodiversity dynamics rather than a simple self-acting response to the filling of the ecological space. It has previously been shown that the filling of the ecological space in the course of diversification is not an automatic process, since evolution under similar conditions routinely produces essentially different life forms (Rasnitsyn, 1987, 2002, 2008) and, therefore, evolution itself is subject to endogenous control. This circumstance in combination with the revealed possibility of endogenous deceleration of evolution can considerably change the generally accepted concept of the evolutionary process.

ACKNOWLEDGMENTS

The work of A.P. Rasnitsyn and D.S. Aristov was supported by the Program of the Presidium of the Russian Academy of Sciences "Problems of the Origin of

Life and Formation of the Biosphere" and by the Russian Foundation for Basic Research, project no. 15-34-20745.

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Translated by P. Petrov