This paper is dedicated to the memory of S.V. Meyen

Permian Faunas of Homoptera (Hemiptera) in Relation to Phytogeography and the Permo-Triassic Crisis

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Abstract—The existing knowledge (including unpublished data) on Permian Homoptera is briefly summarized. Their diversification, faunal composition, geographic distribution and possible host plant associations in the Permian (including the Permo–Triassic transition) are analyzed at the family level. Some peculiarities of the Permo-Triassic crisis are discussed.

INTRODUCTION

The order Hemiptera (bugs, cicadas, hoppers, and plantlice), sometimes divided into two orders, Homoptera and Heteroptera (true bugs), is a large and ancient group of insects richly represented in entomofaunas since the Early Permian. All the Hemiptera possess highly developed piercing-and-sucking mouthparts; virtually all Homoptera are specialized phytophages (now only terrestrial). In the Permian only Homoptera occurred (Heteroptera, including aquatic forms, appeared in the Triassic). The Permian Homoptera are especially advantageous for comprehensive study, because: (a) from the very beginning they were closely associated with their host plants, presumably Mesophytic gymnosperm lineages; (b) having appeared in the Early Permian, they underwent rapid diversification during the Late Permian and a considerable extinction at the Permo-Triassic (P-T) boundary; (c) depending on both climate and vegetation, they demonstrate a definite geographic distribution at the family level in the Late Permian; (d) they mostly possessed stiff forewings that are readily preserved in the fossil state, so they are quite abundant in the paleoentomofaunas; and (e) they are easily identifiable due to their highly diagnostic venation.

Permian Homoptera are known from some fifty localities (total ca. 2800 specimens), mostly from Russia (ca. 40 localities and 2200 specimens), also in a few localities from Mongolia, Kazakhstan, USA, Australia, South Africa, Brazil, and France, the remaining few specimens from Czechia, China, India, Mexico, and even Antarctica. Besides the published data, the present paper is based on the analysis of the collections deposited in the Paleontological Institute, Moscow (PIN), which contains numerous still undescribed fossils. These data were partly used in a review of the Permian entomofaunas (Ponomarenko and Sukatsheva, 1998).

TAXONOMIC NOTES

The system and phylogeny of the extinct Homoptera follow Shcherbakov (1984, 1996). The below taxonomic changes are proposed herein:

(1) the family Prosbolecicadidae is synonymized under Prosbolidae (=Prosbolecicadidae Pinto, 1987, syn. nov.; the genus *Prosbolecicada* Pinto, 1987 is closely related to *Prosbole* Handlirsch, 1904);

(2) the family Fulgoringruidae is included into Dysmorphoptilidae as a subfamily Fulgoringruinae Pinto, 1990, stat. nov.;

(3) the genera *Furcascytina* Lin, 1982 and *Rhipiscytina* Lin, 1982 are transferred from Scytinopteridae, and the genus *Scopiprosbole* Lin, 1982 from Prosbolidae, all to Ignotalidae;

(4) the Permian and Triassic Fulgoroidea (*Surijokocixius* Becker-Migdisova, 1961; *Scytocixius* Martynov, 1937; *Boreocixius* Becker-Migdisova, 1955; *Tricrosbia* Evans, 1971) are separated into the family Surijokocixiidae Shcherbakov, fam. nov., distinct from Fulgoridiidae (known since the Jurassic) in the more distal branching of R and CuA and in the basally widened precostal carina in the forewing (the family name without reference to the diagnostic characters was published earlier: Shcherbakov 1996).

MAIN LOCALITIES OF PERMIAN HOMOPTERA WITH NOTES ON THEIR AGE

In the history of the Earth the cryoeras with climatic zonality comparable to the present day alternate with thermoeras when the latitudinal temperature gradient is decreased (Chumakov, 1993). The Permian was a period of climatic zonality no less marked than at present, and the same ten major biomes (zonobiomes) were defined for both periods (Ziegler, 1990). Phytochorial differentiation was even more pronounced in
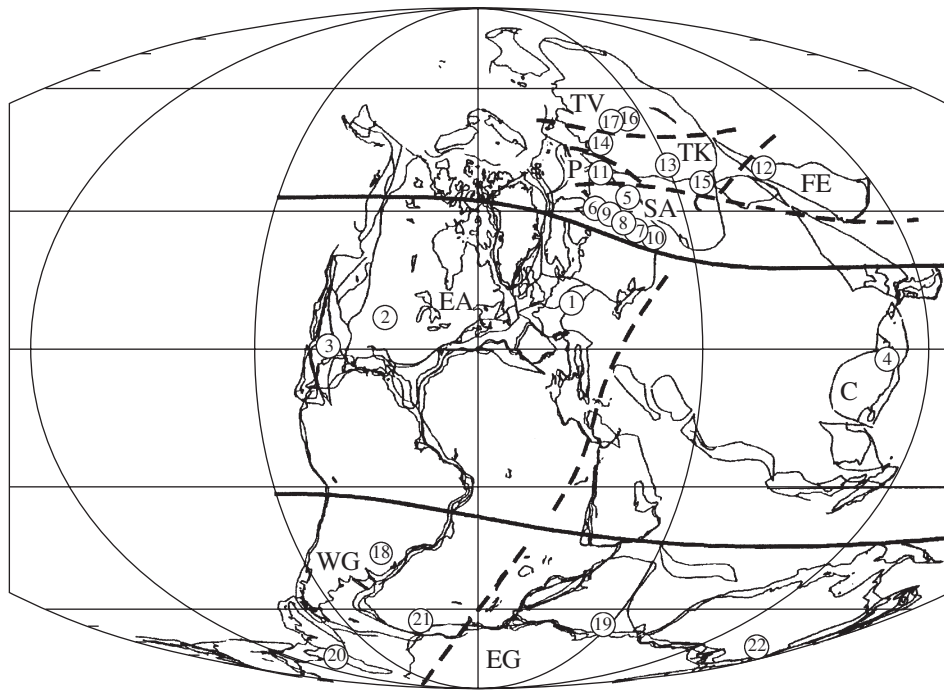
Fig. 1. Permian phytochoria and selected localities of Homoptera (for abbreviations of phytochoria and locality numbers see the text); the Late Permian plate tectonic reconstruction (260 Ma) is from Scotese (1994), slightly modified: Amuria shifted close to Angaraland (similar to in Zharkov and Chumakov, in press) as implied by the floral data (Rees *et al.*, 1999).

the Permian: north (Angarian) and south (Gondwanian) temperate paleofloras were dominated by different gymnosperm groups; in the tropics the floras of Eurameria (EA) and Cathaysia (C) differed strikingly; the temperate Gondwanian Realm was subdivided into the western (WG) and eastern (Australo-Indian, EG) parts (Meyen 1987). Since the Early Permian a Subangarian belt (SA) was formed around the Angaraland, being transitional (ecotonous) to a certain extent between the latter and the tropical zone; in the Kolchuginian time (since the Kazanian, as correlated by Meyen, 1974, see below) the Angaraland proper (Siberian Region) was subdivided into several latitudinal paleofloral zones: the marginal Pechora (P) and Far Eastern (FE) Provinces, the outer Taimyr-Kuznetsk (TK) Subregion, and the inner Tunguska-Verkhoyansk (TV) Subregion, the latter with cold temperate Tunguska and subpolar Verkhoyansk Districts (Meyen, 1970; Durante, 1995). The Subangarian flora (occupying areas bordered by Paleotethys and epicontinental seas) included, besides the typical Angarian plants, also the Euramerian or Cathaysian ones and was especially rich in the Mesophytic elements (Meyen, 1987).

The few known Early Permian Homoptera localities are all situated at low paleolatitudes (up to 35°). Late Permian localities are much more numerous and mostly confined to temperate paleolatitudes (30°–65°), being virtually absent in the tropics. Representative Permian homopterofaunas (HFs) are known mostly in Angaraland, Subangara and Gondwana (Fig. 1). Supposing

that the geographic distribution of land plants and their specialized phytophages is similar, the localities of Homoptera are grouped below in accordance to phytochoria (map localities are numbered in the text).

The Permian standard scale and its correlation with the North American and Tethys scales follows Kotlyar (1997). On the recent estimates the Kazanian was one third of the duration of the Tatarian (5 and above 15 Myr, respectively: Menning, 1995), that agrees with the tendency to lower the boundary between these stages in the Angaraland sections (an extreme version see Shelekhova, 1998). On the Russian platform there is a depositional gap between the Tatarian (Vyatkian) and the Triassic, usually considered as large as the Dorashamian (or Changhsingian) or even greater, whereas in some other regions the P-T section is more complete (Gomankov, 1992). The end-Permian localities (presumably of the Vyatkian and post-Vyatkian age) are marked with an asterisk below.

Euramerian Region (Realm in the Late Permian). Homoptera are absent in the representative Asselian entomofauna from Germany (Hörnschemeyer, 1999). The earliest members of the order were mentioned, but not described, by Kukalová (1964) from the rich entomofauna of **Obora** (1) collected in the Middle Bač ov Beds, Boš covice Furrow, Czechia, considered Lower Sakmarian (Schneider *et al.*, 1995, text-fig. 2; Zajic, in press; sometimes the Artinskian age was given without explanation: Kukalová-Peck and Willmann, 1990). In a small selection of insects from Obora a single wing of

Table 1. Composition of the representative Permian homopter of aunas (percentage abundance from total Homoptera specimens; +, less than 1 percent). Paleolatitude estimates mainly after Ziegler *et al.* (1997). Abbreviations of phytochoria see the text. Biomes (after Ziegler 1990, Rees *et al.* 1999): 4, winterwet; 5, warm temperate; 6, cool temperate; 8, cold temperate. Age abbreviations standard; pv, post-Vyatkian. n/N, no. of families/total no. of hemipteran specimens. Taxa (in the order of appearance): *Archescytinidae*, *Boreoscytidae*, *Coleoscytoidea*, *Prosbolopseidae*, *Ingruidae*, **Pereboriidae**, **Prosbolidae**, **Protopsyllidiidae**, **Dysmorphoptilidae**, **Scytinopteridae**, Serpentivenidae, Surijokocixiidae, Dunstaniidae, Stenoviciidae, Ignotalidae, Paraknightiidae, Pincombeidae, Progonocimicidae (taxa of Group I in *italics*, of Group II in **bold**)

Taxa					*Arc*	*Bor*	*Col*	*Pbp*	*Ing*	**Per**	**Pbl**	**Psy**	**Dys**	**Scy**	Ser	Sur	Dun	Ste	Pkn	Pgn	Ign	Pin	n/N
Locality	Lat.	Flora	Biome	Age																			
Chekarda	35°N	SA	4	kg	90	+	1	3	6														5/600
Soyana	40°N	SA	4	kzl	10	2	2	19	1		53	+	+	13									9/845
Tikhie Gory	30°N	SA	4	kzl	3		7				70			20									4/60
Kityak	35°N	SA	4	kz2			2	4		2	78			13									5/47
Bor-Tolgoy	40°N	FE	5	t1	3	+	3	2	4	11	57			18			+	1					10/240
Karaungir I	50°N	TK	6	t2v					10		30		10	50									4/10
Karaungir II	50°N	TK	6	t2v	2			?2	5	9	75	5		2	2		?1						9/61
Kaltan	50°N	TK	6	kzl	9			7	7	4	17			55									6/242
Sarbala	50°N	TK	6	kzl	18						9			73									3/11
Suriekova I	53°N	TK	6	kz2?							35	5		20	15	25							5/22
Sokolova II	55°N	TK	6	t2s							74		7	14					5				4/43
Ngesankan	65°N	TV	8	t1							36							64					2/11
Kerbo-1	65°N	TV	8	t2s																100			1/300
Mooi	60°S	WG	6	pv?							6	6					22				67		4/17
Belmont	65°S	EG	8	pv?	4						49	27	1				1	9	1	1		7	9/100

a member of the very small Archescytinidae with primitive venation was found by the author; apparently Homoptera were represented only by archescytinids (as in the Elmo fauna), but they were not abundant yet, a fact consistent with the opinion about the older age of the Obora deposits. In the rich Late (?) Artinskian entomofauna from the Lower Leonardian of Kansas and Oklahoma (**Elmo** (2) and several nearby localities of the same age) Homoptera are common and include only moderately diverse Archescytinidae (Tillyard, 1926a; Carpenter, 1947; Tasch and Zimmerman, 1962). Undescribed Homoptera were mentioned from several levels and localities in the **Salagou Formation**, Lodéve Basin (southern France) dated as Sakmarian–Kazanian (Gand of *et al.*, 1997). A doubtful reference to an undescribed member of Scytinopteridae from the Red Tanks Member of **Carrizo Arroyo** (Late Carboniferous–Permian, New Mexico; Rowland, 1997) needs to be confirmed (A.P. Rasnitsyn, pers. comm.). One specimen of Scytinopteridae was found in the Capitanian of Coahuila, Mexico (**Valle de Las Delicias** (3): Carpenter and Miller, 1937; correlated with Lower Tatarian).

Cathaysian Realm. Few specimens of Ignotalidae are known from the **Lungtan Formation*** (4) of South China (Lin, 1982; Wuchiapingian, correlated with Upper Tatarian).

Angarian Realm: Subangarian Region. This is the only phytochoria where the representative HFs are found in both the Early and Late Permian. Homoptera are unknown from the rich early Early Permian (Sakmarian–Artinskian) entomofaunas of North China (Hong 1998). This group is first recorded and common in the rich latest Early Permian (Late Kungurian, Irenian Horizon) entomofauna of Cisuralia (**Chekarda** (5) and other localities: Ponomareva *et al.*, 1998; for composition of the representative HFs see Table 1). The Early Kazanian HFs are found in Arkhangelsk Region (several outcrops of Iva-Gora Formation along the **Soyana River** (6) and its tributaries: Martynov, 1928, etc.) and Tatarstan (**Tikhie Gory** (7) at the Kama River: Handlirsch, 1904, etc.). The Late Kazanian HF is known from the Vyatka River Basin: (Bol'shoi) **Kityak** (8) (on the age see Meyen, 1997). Tatarian finds are scarce: few specimens from the rich Early Tatarian entomofauna of **Kargala** (10) (Martynov, 1937; on the age see Meyen, 1997), one more from the Early Tatarian of **Tuyumbetovskii** (=Saraktash; on the age see Kon'kov, 1967), and few from the early Late Tatarian (Severodvinskian) of (Novo-)**Aleksandrovka** and **Isady** (=Mutovino; on their age see Gomankov and Meyen, 1986) (the latter locality in Vologda Region, three former in Orenburg Region). Several specimens are collected in the lowermost Astashikha Member (**Nedubrovo*** (10)), traditionally assigned to the lowermost Triassic, but now correlated with the Upper Changhsingian of South China (Kozur, 1998) and with the intertrappean deposits of the Tunguska Basin and considered transitional from the Permian to the Triassic (Krassilov *et al.*, 1999).

Pechora Province. Several specimens were collected from the Lekvorkuta Formation (Rudnik Subformation, Kungurian–Ufimian), Inta Formation (Ufimian), Ust'-Perebor Formation (Kazanian), and Pechora Series (Kazanian–Tatarian; ages after Pukhonto, 1996) of the **Vorkuta Coal Basin** (11) and adjacent territories; no Homoptera are found among the insects from older deposits.

Far Eastern Province. The numerous and very diverse Homoptera were collected in the Tsanhi Formation of South Mongolia (**Bor-Tolgoy** (12)) and a few more (belonging to the same genera) in the overlying coal-bearing **Tavan-Tolgoy Formation** (Ponomarenko and Sukatsheva, 1998). These formations contain similar Kolchuginian-type floras, in the combination of ruflorias with sulcial cordaites analogous to the Early Tatarian flora from the Lenino Horizon of Kuznetsk basin; such a correlation is far from reliable due to the earlier appearance of sulcial cordaites in more arid environments (Durante, 1976 and pers. comm.; e.g., sulcial *Cordaites insignis* (Radcz.) S. Meyen in the Early Kazanian of the Russian Platform: Esaulova, 1998), but in this case the paleoclimate was presumably more humid than in Kuznetsk Basin. Tatarian age is confirmed by the finds of Stenoviciidae and Dunstaniidae. The Amuria terrane (to which the locality belongs) is shown in various position in the different plate tectonic reconstructions for the Late Permian: in the most popular versions it is widely separated from Siberia by the ocean and adjacent to the North China terrane (e.g., Ziegler *et al.*, 1997); however, the floral similarity of South Mongolia to Angaraland indicates that the reconstruction should be modified to position Amuria closer to Siberia (Rees *et al.*, 1999; see Fig. 1).

Taimyr-Kuznetsk Subregion. **Kuznetsk Coal Basin** (13) is the only region in the world where a sequence of representative entomofaunas spanning for part of the Carboniferous and the whole of the Permian is known (Rohdendorf *et al.*, 1961). Homoptera are absent in the Balaknonka Series (*Archeglyphis* Martynov, 1931 and *Blattoprosbole* Becker-Migdisova, 1958 belong elsewhere), except for a single archescytinid nymph from the Usa Horizon. In the Kolchugino Series they become abundant and are known from about dozen localities; the representative HFs are found in the Mitino (**Kaltan**, **Sarbala**), Kazankovo-Markino (**Suriekova I**) and Gramoteino Horizons (**Sokolova II**). The Mitino entomofauna (as well as one specimen from the underlying Starokuznetsk Horizon) is the most similar to the Lower Kazanian one from Soyana, but the beetles found there are as derived as the Upper Kazanian ones from Kityak (Ponomarenko and Sukatsheva, 1998), several homopteran genera and species are more derived than their close relatives from the Russian Platform (Table 2), and the abundance of the primitive family Prosbolopseidae (ancestral for the infraorder Cicadomorpha, see Fig. 2) is much lower in Kaltan than in Soyana. Therefore the entomofauna of the Mitino Horizon confirms the late Early Kazanian age suggested by

some paleoflorists (Meyen, 1970, 1974; Pukhonto, 1996) instead of the traditionally accepted Ufimian (correspondingly the Starokuznetsk Horizon could be correlated with the earliest Kazanian and the Usa Horizon to the Ufimian). This shift in the date estimate makes an Early Tatarian age probable for the Uskat Horizon and possible even for the Kazankovo-Markino Horizon (both usually considered Late Kazanian). In these horizons the primitive homopteran families (Group I, see below) are absent whereas Serpentivenidae, Surijokocixiidae and the derived prosbolid genus *Orthoscytina* Tillyard, 1926 are found (not recorded in the Kazanian of other regions); Conchostraca in the latter horizon are similar to those of the Tatarian of the Russian Platform (Bogomazov *et al.*, 1996). The Gramoteino Horizon is correlated with the Severodvinskian (Durante, 1989).

Two more localities are assigned to this phytochory: **Ust'-Port*** (14) in Gyda Peninsula, Western Siberia (Miroshnikov and Pirozhnikov, 1956) correlated with the intertrappean deposits of the Tunguska Basin on the basis of Conchostraca (G.N. Sadovnikov, pers. comm.) and **Karaungir I** and **II*** (15) in the Kenderlyk Syncline, Eastern Kazakhstan (uppermost Maichat and basal Akkolka Formations, respectively) correlated with the Vyatka Horizon on the basis of Conchostraca (Novozhilov, 1970); the upper part of the Akkolka Formation is sometimes considered Triassic (Vorontsov, 1961), but it contains a Kolchuginian-type flora (Meyen, 1970) and coal seams; the higher diversity of Homoptera relative to the other localities in this phytochory could be explained by the lower paleolatitude and the end-Permian age.

Tunguska-Verkhoyansk Subregion. The material from Tunguska Basin (Tunguska District) is not rich; insects are not recorded from the subpolar Verkhoyansk District. There are several localities in coal-bearing, undoubtedly Upper Permian deposits with a cordaitean flora: in the Pelyatka Horizon (few specimens in **Pelyatka** and **Tanka**), Degali Horizon (?) (**Ngesankan**; due to the presence of *Orthoscytina* sp., very similar to *O. pallida* Becker-Migdisova, 1961 from the Uskat Horizon (Lower Tatarian?) this locality could be correlated with the latter; the presence of Stenoviciidae confirms the Tatarian age), and Gagarii Ostrov Horizon (**Kerbo-1** and **Neptenne-2** (16); due to the presence of Paraknightiidae could be correlated with the Gramoteino Horizon (Severodvinskian)); no Homoptera are found among the insects from the older deposits. Scarce but very interesting finds are made in the overlying intertrappean deposits with Korvunchanian flora (Dvurogino and Putorana Horizons): lower Bugarikta Formation (**Nizhnyaya Bugarikta***, Archescytinidae); Limptekon Formation (**Ukshunukan***, Ignotalidae); upper Nidym Formation (**Severnoe Lake*** (17), Ignotalidae, *Rhipiscytina* sp.; on the locality see Mogucheva, 1973); lower Kochechumo Formation (**Untuun-2***, Dysmorphoptilidae; on the locality see Novozhilov, 1970); stratigraphic position of one more find of Igno-

Table 2. Selected taxa of Cicadomorpha from the Iva-Gora Formation and their more derived counterparts from the Mitino Horizon

Family	Iva-Gora Formation	Mitino Horizon
Prosbolopseidae	*Anaprosbole* B.-M.	*Prosboloneura* B.-M.
	Prosbolopsis Mart.	*Kaltanopibrocha* B.-M
Ingruidae	*Ingruo* B.-M.	*Permododa* B.-M.
Prosbolidae	*Sojanoneura* Mart.	*Kaltanetta* B.-M.
	Prosbole Handl.	*Evanscicada* B.-M.
	Permocicadopsis B.-M.	*Kaltanopsis* B.-M.
Scytinopteridae	*Scytinoptera kokeni* Handl.	*S. sibirica* B.-M.

talidae from the **Kureika River*** is unclear. These deposits were variously dated either as the Early (or even Early plus Middle: Dobruskina, 1989) Triassic, or (at least partly) as the latest Permian (e.g., Sadovnikov, 1981). Based on the new data the eruption of the Siberian Traps was rapid (less than 1 Myr), coinciding with culmination of the P-T life crisis (the boundary beds and the base of the Triassic on magnetostratigraphic data), and was possibly its proximal cause (Renne and Basu, 1991; Campbell *et al.*, 1992; Bowring *et al.*, 1998). Presence of the homopteran families not recorded in the unquestionably Triassic strata (ignotalids from the Nidym Formation were erroneously mentioned as Triassic Auchenorrhyncha: Ponomarenko and Sukatsheva, 1998) and the absence of post-Permian hemipteran groups agrees with assignment of the intertrappean deposits to the P-T boundary.

Gondwanian Realm. Several specimens were collected from the **Irati Formation** (18) (Kazanian; Pinto, 1972, 1987, 1990; Pinto and Ornellas, 1981; Pinto and Adami-Rodrigues, 1999) and the **Rio do Rasto Formation** (latest Permian–earliest Triassic; Martins-Neto and Rohn, 1996) of the Paraná Basin, Brazil. The finds of Ignotalidae in the **Ironstone Shales** (19) of the Kulti-Raniganj Field, North-East India (J.W. Schneider, pers. comm.) and of Stenoviciidae in the **Polarstar Formation** (20) of Sentinel Mountains, West Antarctica (Tasch and Riek, 1969) indicate the Tatarian age of these deposits. A diverse end-Permian HF is known from the *Daptocephalus (=Dicynodon)* zone (Lower Beaufort Series) of the northern Karoo Basin, Natal (**Mooi River*** (21) and other localities*; Riek, 1973, 1974, 1976), correlated with the Dzhulfian (Anderson, 1977) or Dorashamian (Ochev, 1999). A rich entomofauna, the only Permian one containing several endemic families (Ponomarenko and Sukatsheva, 1998), is known from the upper Newcastle Coal Measures of the Sydney Basin, East Australia (**Belmont*** (22), Eleebana Formation; Tillyard, 1926b; Evans, 1956; etc.); these deposits were correlated with the Vyatka Horizon on the basis of Conchostraca
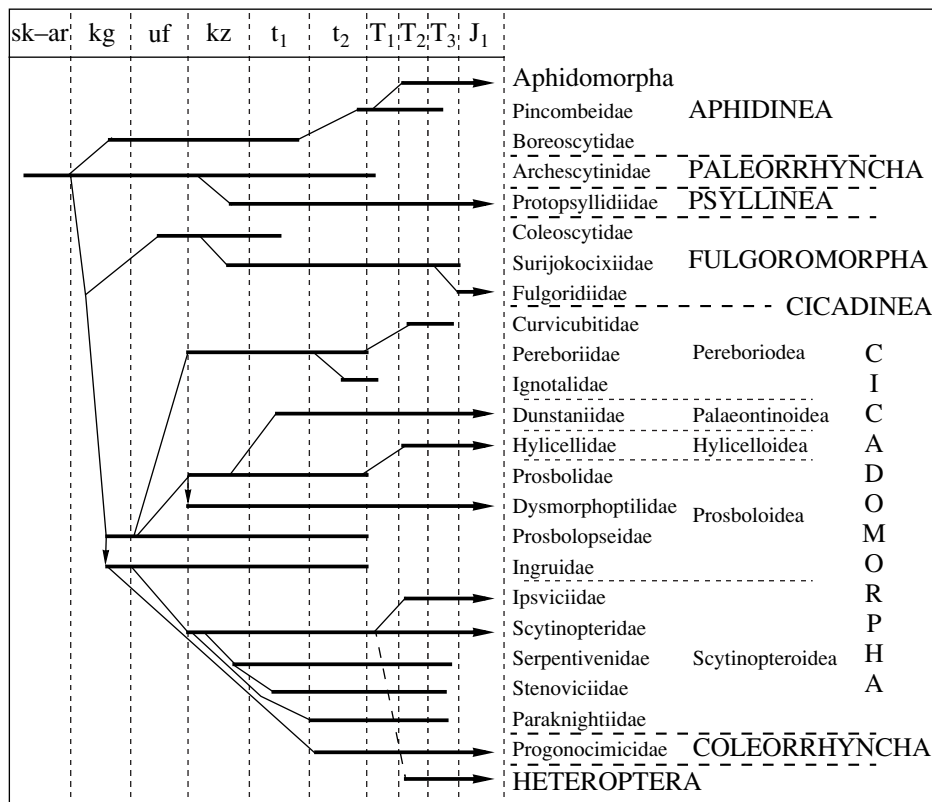
Fig. 2. Phylogeny and stratigraphic range of the Permian and Triassic Hemiptera.

(Novozhilov, 1970), but could be post-Vyatkian (Changhsingian) in age (Foster *et al.*, 1998).

DIVERSITY

The oldest (known since the Sakmarian) and ancestral suborder of Hemiptera, Paleorrhyncha (=Archescytininea), is believed to descend from the Paleozoic order Hypoperlida (Rasnitsyn, 1980). Two other suborders, Aphidinea and Auchenorrhyncha (=Cicadinea), enter the fossil record in the Kungurian (the latter as two phyletic lineages at once, the infraorders Fulgoro- and Cicadomorpha), and two more, Psyllinea and Coleorrhyncha (=Peloridiinea), in the Kazanian and Tatarian respectively (Popov and Shcherbakov, 1991, 1996; Shcherbakov 1990, 1996). All these suborders (constituting the paraphyletic Homoptera) are mostly phytophagous (rarely mycetophagous), in contrast to the remaining (sixth) suborder, Heteroptera (=Cimicinea), containing numerous myxo- and zoophages and appearing in the Middle Triassic.

Paleorrhyncha, currently comprising only one family, Archescytinidae, demonstrate a striking diversity in the head and ovipositor structure (contrasting with quite uniform venation), probably sufficient to divide this group into several families after detailed study. The difference in the position of the rostrum base, comparable to that between the suborders Auchenorrhyncha and Heteroptera, gives an example of the archaic variety within this ancestral suborder. In the Early Sakmarian (Obora) the oldest archescytinid wing is found, in the Artinskian (Elmo fauna) all the Hemiptera were archescytinids, and by the Kungurian the group reached its peak diversity and abundance, demonstrating the first radiation in hemipteran history.

Besides archescytinids, the first Auchenorrhyncha (3 families) and Aphidinea (1 family) are recorded in the Kungurian. The number of families increased almost exponentially from the Kungurian (5) through the Kazanian (10) up to the Tatarian (19 families). An evolutionary potential of the Permian families correlates with their age: of six families known prior to the Kazanian, one (undescribed coleoscytoids) is endemic of the Kungurian and five others became extinct about the P-T boundary; of 14 families appearing in the Kazanian or Tatarian, 12 survived into the Triassic, six of them giving rise to the extant sub- or infraorders and one more to a prolific Mesozoic superfamily (Fig. 2; stratigraphic range of the families see also Table 3).

Therefore the hemipteran phyletic radiation in the Permian could be subdivided into three or even four stages: archescytinid diversification (Sakmarian–Kungurian), origin of three other sub- and infraorders (Kungurian), origin of the families dominant in the Late Permian (earliest Kazanian), and rise of the Mesozoic groups (mainly Tatarian). Hereafter for the further anal-

Table 3. Known distribution of homopteran families across the Permian phytochoria. Phytochoria with better known homopterofauna in **bold** (abbreviations see the text). Age: for taxa, known stratigraphical range; for phytochoria, age of known homopterofaunas. 0, supposed biogeographically significant absence; (?), doubtful finds; *, Prosbolidae incl. *Orthoscytina*. Taxa of Group 1 in *italics*, of Group 2 in **bold**

	Phyto-chory	TV	TK	P	FE	SA	EA	C	WG	EG
Taxon	**Age**	t–pv	uf–pv	uf–t	t1	kg–pv	P1, t	t2	kz–pv?	t, pv?
Archescytinidae	sk–pv	pv	uf–kz, t2v	uf	+	kg–kz1, pv	sk, ar			pv?
Boreoscytidae	kg–t1?	0	0		+	kg–kz1				
Coleoscytoidea	kg–t1?	0	0	uf	+	kg–kz2				
Prosbolopseidae	kg–t2	0	kz, t2v	uf	+	kg–kz2				
Ingruidae	kg–t2	0	kz, t2v		+	kg–kz1				
Pereboriidae	kz1–t1?	(?) kz2	kz, t2v	kz	+	kz2–t1			kz	
Prosbolidae	kz1–pv?	kz2–t1	kz–t2v*	t1	+*	kz1–kz2	0	0	kz, *pv?	*pv?
Protopsyllidiidae	kz1–K2	0	kz2?, t2v		0	kz1			kz, pv?	pv?
Dysmorphoptilidae	kz1–J3	pv	t2s–v		0	kz1			pv?	pv?
Scytinopteridae	kz1–K1	0	kz–t2v	kz–t	+	kz1–t2s	t1		0	0
Serpentivenidae	kz2?–T2/3	0	kz2?, t2v		0				0	0
Surijokocixiidae	kz2?–T3		kz2?, pv		0	t1			0	0
Dunstaniidae	t1?–J1	0	(?) t2v		+				pv?	pv?
Stenoviciidae	t1?–T2/3	t1	0		+	(?) pv			t	pv?
Paraknightiidae	t2s–T2/3	t2s	t2s				0	0		pv?
Progonocimicidae	t2s–K2		0			t2s				pv?
Ignotalidae	t2–pv	pv	0					t2	pv?	t
Pincombeidae	pv?–T3		0							pv?

ysis, all the Permian families are divided into three groups as follows: Group I, first recorded in the Sakmarian–Ufimian: Archescytinidae, Boreoscytidae, Coleoscytidae (and one more, undescribed coleoscytoid family), Prosbolopseidae, and Ingruidae; Group II, first recorded in the Early Kazanian: Pereboriidae, Prosbolidae, Scytinopteridae, Protopsyllidiidae, and Dysmorphoptilidae; Group III, the remaining nine families appearing later.

The change of hemipteran family composition about the P-T boundary seems more abrupt than those changes at the Jurassic–Cretaceous or Cretaceous–Paleogene boundaries (this is only partly due to the lack of knowledge on the Early Triassic Hemiptera). Possibly some families are not found in the Late Tatarian just because of the marked decrease in their range and abundance; this results in underestimation of the extinction at the P-T boundary (Signor–Lipps effect: Signor and Lipps, 1982). Scarcely more than a half the homopteran families known in the Permian (11 of 20) survived into the Mesozoic (including **none** of the Group 1 families, i.e., of pre-Kazanian origin), whereas the extant families constitute about 1/5 of total homopteran families in the Late Jurassic and about a half of those in the Late Cretaceous (the changes about the Jurassic–Cretaceous boundary were the most significant since the Liassic:

Shcherbakov and Wegierek, 1990). In Homoptera these repeated faunal overturns have been at least partly caused by evolutionary changes in the host plant lineages, in contrast to predominantly zoophagous Heteroptera, which show a negligible extinction at the family level since the Liassic.

TAPHONOMY

Unlike many other insect orders, Hemiptera are extremely diverse and therefore not subject to the same taphonomic rules. Archescytinids, with membranous wings, were initially small (up to 5 mm long), but gave rise to Auchenorrhyncha which had already diversified in size (from 3 to 50 mm long) and habitus by the Kazanian. In the Late Permian large and giant cicadas (known from the wings only) had first appeared; they were not directly related to the present-day singing cicadas. Some genera of Prosbolidae, Pereboriidae, and finally Ignotalidae reached about the same size (wingspan ca. 230 mm) as the largest Mesozoic and recent Auchenorrhyncha; Permian Dunstaniidae were quite small. It is supposed that in many oryctocoenoses the remains of small or (rarely) of large insects predominate due to differential water transport; although large cicadas are not found in most of the Tatarian localities
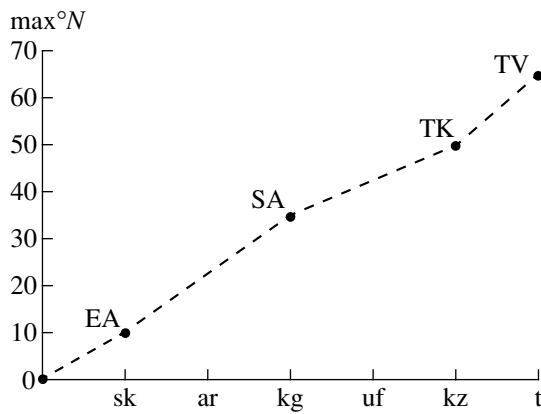
Fig. 3. Increase in paleolatitude of the northernmost discovering of representative homopterofaunas during the Permian.

of the Kuznetsk and Tunguska basins, this can be explained in terms of biogeography.

On the other hand, Auchenorrhyncha with strongly sclerotized forewings (mostly of small size) began to appear from the Ufimian: Coleoscytidae, Dysmorphoptilidae, some genera of Prosbolidae, and especially Scytinopteroidea (their forewings enveloped the abdomen similar to beetle elytra). Such forms, like beetles and cockroaches, are over-represented in oryctocoenoses, because their isolated forewings are readily preserved in the fossil state. Among them Scytinopteroidea merit special consideration. They had already acquired the modified "knob" mechanism for the forewing fixation on the mesopleuron, shared with their descendants, Heteroptera (Popov and Shcherbakov, 1991; Shcherbakov, 1996). Association with water is widespread among primitive Heteroptera and may have been characteristic of ancestral bugs. By analogy to the most primitive true bugs (Nepomorpha), the knob fixation in scytinopteroids could be interpreted as an adaptation for subelytral air storage, and therefore evidence of a lifestyle more amphibiotic than in any other Homoptera. Probably scytinopteroids lived in waterside vegetation, so their abundance in many localities is further exaggerated. Their descendants, shore, amphibiotic and water bugs are even more over-represented in many Mesozoic oryctocoenoses.

The supposition about a waterside mode of life in Scytinopteroidea is confirmed by two more facts. The identical entomofaunas of Kerbo-1 and Neptenne-2 (Tunguska Basin) consist almost entirely of numerous nymphs and few adults of a single species of Paraknightiidae (both abundance and the instar proportion being unusual for truly terrestrial insects), whereas the copious plant megafossils in the Kerbo-1 insect bed almost all belong (V.V. Zherikhin, pers. comm.) to the equisetalean *Phyllotheca turnaensis* Gorelova (Tchernoviaceae; Meyen, 1971); co-occurrence of numerous flightless nymphs and well preserved horsetails testifies

that both were buried autochthonously in the shore biotope and that these hoppers fed on the horsetails. Permian sphenophytes formed the shore vegetation similar to the present-day sedges and rush.

In the Karaungir locality (East Kazakhstan) Scytinopteridae dominate in the lower insect bed (Karaungir I) and Prosbolidae in the upper one (Karaungir II); these beds are separated by a rather short time interval (Novozhilov, 1970), but the former bed represents the near-shore facies whereas the latter the off-shore one (A.G. Ponomarenko, pers. comm.; the insect bed of Kaltan locality is possibly also of near-shore origin). Prosbolids and scytinopterids predominate in most HFs of Angaraland and Subangara, their percentage abundances being anticorrelated and each much more varying (9–78 and 73–2 per cent, respectively) than their common share (55–91 per cent); if Scytinopteridae were indeed associated with helophytes, it is reasonable to assume that Prosbolidae inhabited biotopes more remote from the water but clearly not the most xerophilous (because this family is absent from the arid Subangara in the Tatarian). If so, in the Kuznetsk Basin oryctocoenoses the decrease of initially quite high scytinopterid abundance from the Kazanian to the Tatarian is explainable in terms of reduction in area of waterside vegetation due to changing climate or relief (being paralleled by the increasing abundance of xeromorphic plants: Betechtina *et al.*, 1988).

BIOGEOGRAPHY

Paleontological data confirm the "ousted relicts" concept going back to Alfred Russel Wallace (Eskov and Golovatch, 1986). Nearly all the higher taxa of vascular plants appear in the equatorial zone and adjacent ecotonous phytochoria, and some taxa after becoming extinct in the tropics persist in the extratropical floras, giving them an archaic aspect ("phytospreading": Meyen, 1987). Analogous latitudinal "polarization" of the phylogenetic lineages is revealed in land arthropods, at least in the zonal epoch of the Late Paleozoic (Eskov, 1995).

The materials available agree with the supposition that Hemiptera originated in the equatorial zone and then gradually colonized the higher latitudes. In the pre-Kungurian Homoptera are known only in Eurameria, since the Kungurian are common in Subangara, and since the Ufimian in the Pechora Basin; in the Kuznetsk Basin they are very rare in the Ufimian and common since the Kazanian, in the Tunguska Basin they are rare in the Late Kazanian and more common in the Tatarian (Fig. 3), and at the equally high paleolatitudes of Gondwana they are known from the end of the Permian. The first finds of more than a half of the homopteran families known in the Permian are confined to the equatorial zone or ecotonous Subangara (underestimation is possible, because Homoptera of the Permian tropics are little known). The paleolatitude of the last Permian find is higher than that of the first find for nearly all these fam-

ilies, except for Coleoscytidae and Serpentivenidae (the latter is known only from rather low palaeolatitudes in the Triassic as well), though most of these families penetrated into the high latitudes only with reduction of latitudinal zonality in the end of the Permian.

Geographic ranges of the homopteran families were different in the Permian (Table 3). Due to extensive aridization of the Late Permian equatorial zone, the insect fossils there are scarce, but one can expect to find there (especially in the humid Cathaysia) those taxa, up to now recorded only from the temperate zones of both hemispheres. Among Homoptera these are (besides Scytinopteridae and Ignotalidae already found) principally the families recorded in both Subangara and temperate Gondwana (the remaining Group 2 families and Progonocimicidae). With aridization of mainly lower latitudes progressing during the Late Permian, equatorial disjunctions were obviously becoming more numerous, and bipolar ranges are probable for Paraknightiidae associated with the waterside plants, and (in the Tatarian) for Prosbolidae (including the genus *Orthoscytina*). The bipolar ranges are recorded in the Permian for many marine invertebrate genera (Ustritskiy, 1974); some insects with apparently bipolar ranges may be found to be in fact of worldwide occurrence when the Permian tropical entomofauna becomes better known.

Archescytinidae are present in all phytochoria, but in the Tunguska Basin and Gondwana only in the end of the Permian, and in the Subangara and Taimyr-Kuznetsk Subregion disappear from the record by the Late Kazanian and reappear for the last time near the P-T boundary. The remaining Group 1 families are known only from Subangara and outer Angaraland, Boreoscytidae and Coleoscytidae not penetrating into Angaraland beyond the marginal provinces, whereas Prosbolopseidae and Ingruidae colonized the Kuznetsk basin in the Kazanian but had vanished by the Tatarian.

The Group 2 taxa are widespread and found in Gondwana as well, except for Scytinopteridae (though found in the tropics) and most of the prosbolid genera. The absence of the latter taxa along with even more generalized Group 1 families (except for archescytinids in the end of the Permian) from the Southern Hemisphere might be caused by the extensive Gondwana glaciation in the Late Carboniferous and Early Permian, during the time of origin and basal radiation of Hemiptera, so the temperate Gondwanian fauna seems to have been formed mostly by the immigrants from the north. However, scytinopterids surviving up to the Cretaceous had already colonized Australia by the Triassic (they are not at this point known from South Africa; the Triassic *"Scytinoptera" distorta* Riek, 1976 was transferred to Progonocimicidae: Popov and Shcherbakov, 1991). In the Late Permian Scytinopteridae had not spread into the Tunguska Basin, Pereboriidae are known there only from a doubtful find, and Dysmorphoptilidae arrived there at the P-T boundary. In the

impoverished Tatarian HF of the Russian Platform prosbolids are not found, and pereboriids are represented by derived forms of *Scytophara*-type. The first records of Dysmorphoptilidae and Protopsyllidiidae are from the Early Kazanian (Soyana: undescribed Fulgoringruinae and *Permaphidopsis* Becker-Migdisova, 1960), but they remain extremely rare up to the end of the Permian when they become dominant in some HFs of Gondwana (both families are common and widespread in the Mesozoic). The widespread family Prosbolidae might have originated on the Russian platform where several generalized genera connected by some transitional forms are known, whereas the prosbolids of the Siberian Region and Gondwana are more derived and less diverse. In the HFs of Angaraland and Gondwana up to the present only one common genus is recorded, *Orthoscytina* (Kuznetsk Basin, Karaungir, Mongolia, Australia, and South Africa), less than in some other, no-phytophagous insect groups (e.g., several common genera of Mecoptera: Novokshonov, 1997).

Of the Group 3 families Stenoviciidae and Paraknightiidae are quite widespread and known also from the Triassic of Eurasia. The most interesting are Ignotalidae, which (like archescytinids) are found both in the tropics and (near the P-T boundary) at high latitudes; moreover, the same range is revealed for the genus *Rhipiscytina* (Lungtan and Nidym Formations); both families are unknown from undoubtedly Mesozoic deposits. In both the north and south temperate zones Progonocimicidae (Belmont and undescribed find from Isady) and Dunstaniidae are found, both families being common and widespread in the Mesozoic of both hemispheres. Pincombeidae appear by the end of the Permian (Belmont) and are also recorded in the Triassic of Europe and Central Asia. Serpentivenidae and Surijokocixiidae are not found in the Permian of Gondwana; surijokocixiids are absent in the Late Tatarian HF of the Kuznetsk Basin and appear at a higher paleolatitude about the P-T boundary (Ust'-Port); both families are common in the Triassic of Central Asia, the latter being also recorded in the Triassic of Australia.

FAUNAL CHANGES AS RELATED TO FLORAL ONES

The regular changes in the composition of HFs during the Permian are revealed (Figs. 4–5). In the pre-Kungurian Homoptera are represented by archescytinids only, first rare, then common. The Kungurian Bardian flora dominated by various conifers and abundant peltasperms (Naugolnykh, 1993) is accompanied by a rich HF, consisting mostly of the very diverse archescytinids (ca. 90 per cent) and including also the earliest known members of the other Group I taxa.

Scarce finds in the Ufimian all belong to the Group I families (Archescytinidae, Coleoscytidae, and Prosbolopseidae; the dominants of subsequent HFs are not found), indicating that the fauna is similar to that of the Kungurian and could be assigned to the same faunoge-
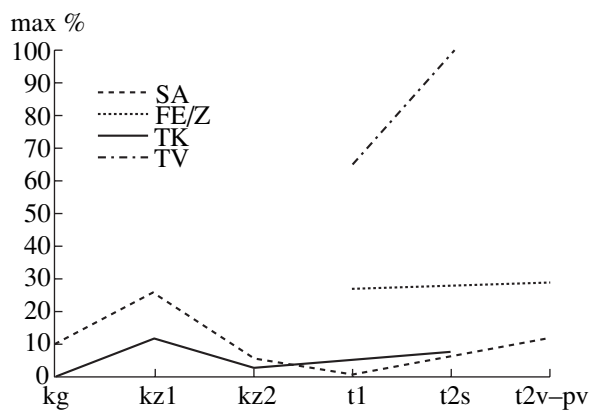
SHCHERBAKOV

Fig. 4. Changes in abundance of Homoptera in the Permian entomofaunas (maximal per cent from total insect specimens) from the Kungurian to the end-Permian in different phytochoria (Z, Karaungir; other abbreviations see the text).
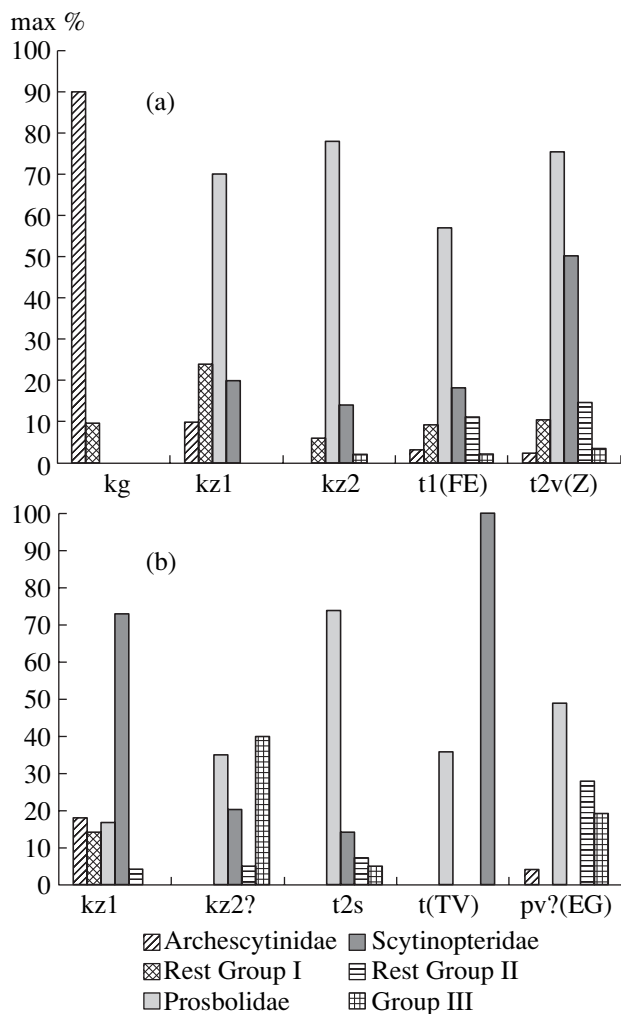

Fig. 5. Abundance of homopteran groups (maximal per cent from total Homoptera specimens) in the entomofaunas of different age and phytochoria: (a) Subangara and marginal Siberian Region (FE, Bor-Tolgoi; Z, Karaungir); (b) Kuznetsk Basin, Tunguska Basin (TV), and Belmont (EG).

netic stage (corresponding to the Middle Permian in one of the versions of tripartite division of the Permian).

On account of paleofloral data the beginning of the Kazanian is marked with a warming which extended to the outer Angaraland, and soon changed into a slight cooling, then into at least one more warming episode, and only by the end of the Permian into the final warming (if not stated otherwise, the floral and climatic changes follow Durante (1995) and biomes follow Ziegler (1990)). In the Kazanian entomofaunas of Subangara and Angaraland the Homoptera become (sub)dominant, Prosbolidae and Scytinopteridae (Group II) prevail over the Group I families (abundance of archescytinids is usually below 10 per cent in the Kazanian and below 5 per cent in the Tatarian). HFs and their changes during the Kazanian–Tatarian reveal some differences according to the floral differentiation.

In Subangara on the **Russian platform** Homoptera flourished in the Early Kazanian (up to 1/4 of the total insects in some oryctocoenoses: Soyana, Tikhie Gory) on the rich conifer-pteridosperm Phylladodermian flora of the winter wet mediterranean biome (with sclerophyllous woody plants). By the Late Kazanian the abundance of the total Homoptera and especially of the Group I families decreased, archescytinids disappeared, and the prosbolid dominance became more marked. In the Early Tatarian the flora of this area was impoverished (composition of pteridosperms renewed, cordaites disappearing from most localities: Esaulova, 1998), and Homoptera became more rare (only 1 per cent in the rich Kargala entomofauna), the Group I families and prosbolids vanished, and Surijokocixiidae and derived Pereboriidae appeared. In the Late Tatarian when the peculiar Tatarinian flora existed (Gomankov and Meyen, 1986), two more Mesozoic families are recorded (Progonocimicidae and an undescribed Triassic one). At the P-T boundary (Nedubrovo) archescytinids are again recorded (for the last time) (the forms similar to those from the intertrappean deposits of Nizhnyaya Bugarikta in the Tunguska basin).

In Angaraland from the Ufimian to Kazanian one geoflora changed into another, callipterids and other Subangarian migrants penetrating into the outer Taimyr-Kuznetsk Subregion. In the **Kuznetsk Basin** the entomofaunas almost entirely consisting of cockroaches (accompanying the pteridosperm-cordaitean and cordaitean geofloras; cockroaches also dominate the Early Permian entomofaunas of North China) were replaced by those dominated by Mecoptera, Homoptera and Grylloblattida (later also Coleoptera) during the existence of the richest fern-pteridosperm-cordaitean Kolchuginian geoflora of the cool temperate biome (with nemoral forests). The earliest rich HFs in this area resemble the Early Kazanian ones of the Russian platform, but differ in containing several more derived genera and in the lower abundance of the Group I families (evidence of the younger age), and also in the scytinop-

terids prevailing over prosbolids (evidence of the broader development of waterside vegetation) and the lower abundance of total Homoptera. Later, in the latest Kazanian–earliest Tatarian, with the climate becoming more continental, changes analogous to those on the Russian platform took place: the abundance of total Homoptera further decreased, prosbolid dominance was restored and then (by the Severodvinskian) increased, the Group I families vanished and those of the Group III appeared.

The HFs of the southern margin of Siberian Region (**Pechora** and **Far Eastern** Provinces, and also **Karaungir** at the margin of the Taimyr-Kuznetsk Subregion) reveal some similarities. In two former HFs (accompanying the floras that contain Subangarian and Cathaysian elements, respectively) Coleoscytidae and Pereboriidae coexist like in the Late Kazanian of the Russian Platform. Two latter HFs are distinct from all the other Permian HFs in the co-occurrence of several families of the Group I (not only archescytinids) and the Group III families, and in the retention of high abundance of total Homoptera into the Tatarian. An unusual diversity of the Bor-Tolgoi entomofauna is explainable by its position at relatively low paleolatitude not far from the sea (Ziegler (1990) even assigned this area to the warm temperate biome with evergreen forests, but it is scarcely possible for this Kolchuginian-type flora). In this entomofauna Palaeodictyoptera are last recorded and Coleoptera from the most primitive to quite derived coexist (Ponomarenko and Sukatsheva, 1998). Therefore, in a favourable maritime climate (not arid as on the Russian Platform, and less continental than in the Kuznetsk Basin) archaic groups might survive up to the end of the Permian, and possibly boreoscytids and coleoscytids were still not found in the Late Tatarian simply due to the marked restriction of their range.

All the insect genera described from the Kazanian of temperate West Gondwana (Paraná Basin) are closely related to those known from the Russian Platform, Pechora and Kuznetsk basins (Pinto, Adami-Rodrigues, 1999). Such a similarity of the synchronous north and south temperate entomofaunas could be retained into the Tatarian; if so, then the difference of Tatarian HFs of Angaraland and Subangara frome those of the Karoo and Sydney basins should be explained by the end-Permian age of the two latter. The Belmont entomofauna is peculiar, possibly because it pertains to the cold temperate biome (Rees *et al.*, 1999; shelf glaciers persisted in the nearby New Zealand up to the Early Tatarian: Ziegler *et al.*, 1998), whereas the climate of the Karoo Basin was moderated by giant lakes (Yemane, 1993). In the end of the Permian in the temperate Gondwana the families of Group III or II dominate (dysmorphoptilids and protopsyllidiids first becoming abundant), and only archescytinids are recorded from Group I.

An impoverished Kolchuginian flora of the cold temperate biome (with boreal forests) from the coal-bearing deposits of the **Tunguska Basin** is accompanied by the very poor entomofaunas. Homoptera (at first the derived prosbolids only) appeared there about the next warming near the Kazanian–Tatarian boundary, along with the first wave of infrequent Subangarian migrants (e.g., *Rhipidopsis* pteridosperms). In the later entomofaunas Homoptera predominate (up to almost 100 per cent), but are represented by one or two species only, the Group III scytinopteroid families associated with the waterside vegetation (stenoviciids and paraknightiids) prevailing. Large cicadas (rare in the Tatarian of the Russian platform and Kuznetsk Basin) are not recorded with certainty.

By the Severodvinskian time the HFs of different latitudinal zones in the Northern Hemisphere became clearly differentiated (like floras), but by the end of the Permian this geographic segregation had been reduced, probably due to disappearance of the polar "freezer" (the last glacial deposits in Kolyma could be of Tatarian age: Chumakov, 1994). The final global warming with destruction of the climatic barriers was possibly caused by the eruption of the Siberian Traps flood basalts at the P-T boundary. In the Tunguska and Kuznetsk basins the floras were completely renewed at the boundary of the coal-bearing and intertrappean deposits: the Kolchuginian flora dominated by cordaites was replaced by the conifer-fern Korvunchanian flora, containing many plants similar to those from the Paleozoic of Eurameria and Cathaysia, as well as the widespread lycopod family Pleuromeiaceae (Dobruskina, 1982, 1989; in the latter paper the floral differences of three intertrappean horizons are considered to be the age differences from the Induan up to Anisian, but the trap eruption scarcely lasted more than 1 MA, so the changes in flora and fauna were related rather to the rapid climatic fluctuations and uplift of the Earth's surface). In the Tunguska Basin the Homoptera of the cold temperate biome (Prosbolidae and derived Scytinopteroidea) were replaced by the immigrants from the lower paleolatitudes: Dysmorphoptilidae, Surijokocixiidae, Archescytinidae and Ignotalidae, the latter family (not recorded north of the equator in the earlier HFs) apparently extended its range more than the others.

Undisputed Early Triassic Hemiptera are unknown. A poor Middle Triassic HF from the Perebor Formation of Pai-Khoy (Ladinian?: Dobruskina, 1982; erroneously attributed to the Early Triassic: Ponomarenko and Sukatsheva, 1998) consists almost exclusively of Scytinopteridae. The post-Permian families are first recorded in the richer Middle Triassic (Anisian) HFs of Vosges, France and Brookvale, Australia.

HOST PLANT ASSOCIATIONS

The beginning of the Permian was marked with an expansion of Mesophytic gymnosperm groups, such as peltasperms (ancestral to ginkgophytes) and conifers (Meyen, 1987). It is hardly a coincidence that soon after that the basal Hemiptera (Paleorrhyncha) had

originated, the chewing mouthparts of their hypoperlid ancestors had become modified into a rostrum to ingest the contents of the plant vascular tissues. Some archescytinids with long ovipositor valves either coiled under the abdomen (Becker-Migdisova, 1960b) or protruding caudad in repose, probably laid eggs into the gymnosperm female cupules and strobili (Becker-Migdisova, 1985), where their flattened nymphs dwelt until the seeds ripened. Similar association with plant reproductive organs is possible also for other archescytinids with the ovipositor less modified. Such a supposition agrees well with the hypothesis that the earliest Pterygota fed on the gymnosperm ovules (Rasnitsyn, 1980). These ovipositor modifications have closer counterparts hymenopterans than in the other hemipterans indicating that archescytinids might be ecological analogs and predecessors of primitive xyelid sawflies whose larvae live in the gymnosperm strobili (Hymenoptera enter the record in the mid-Triassic, after the extinction of Archescytinidae about the P-T boundary).

As living Homoptera are mainly confined to seed plants and all the instances of colonizing cryptogams may be interpreted as secondary, it is reasonable to assume that gymnosperms were the hosts of the basal Hemiptera. Changing over to the sucking of the plant reproductive organs is supposed from palinophagy, and notably in the gut contents of Kungurian insects (three orders, including Hypoperlida ancestral to Hemiptera, and Psocoptera related to them) the pollen of various gymnosperms is found (and no spores; Krassilov and Rasnitsyn, 1999).

The example of Paraknightiidae shows that already in the Permian the homopterans colonized sphenophytes (and possibly some other groups of spore plants). The phyletic lineages for which the xylem- or mesophyll-feeding could be supposed, are known no earlier than in the Mesozoic, so the Permian Homoptera most probably sucked from the phloem and the plant reproductive organs; if so, they could be mostly associated with certain host plant groups, because the broad polyphages are known now mainly among the xylemotrophs. However, already by the end of the Permian some derived genera found in the widely separated localities with quite dissimilar floras (closely related species of *Orthoscytina* in Kazakhstan and Natal, *Rhipiscytina* spp. in South China and Tunguska) presumably had a wide range of the host plants. More detailed analysis of geographic and stratigraphic distribution of the Permian plants and Homoptera is needed to elucidate their trophic relations, though some assumptions could already be made.

Archescytinids are mainly confined to the floras with a considerable abundance of conifers (Euramerian, Subangarian, Korvunchanian, Nedubrovo) and might be associated with them; presence of these insects in some localities with the Kolchuginian flora (lacking undoubted conifer megafossils) indicates either the different host plants for some archescytinids

or the presence of conifers on watersheds remote from the place of burial. The presumed relation to conifers is in agreement with two more facts: the conifer pollen predominates in the gut contents of Kungurian Hypoperlidae (archescytinid ancestors) and related Psocidiidae (Krassilov and Rasnitsyn, 1999); conifers are the host plants for several primitive groups of Aphidinea, the lineage descending from archescytinids via Pincombeidae and Boreoscytidae (Shcherbakov, 1990).

Feeding homopterans stay in one place for a long time, and large cicadas can find shelter only in large-leafed arboreous plants. The Permian conifers had needle-like leaves, and the small size of all the earliest (Kungurian) Auchenorrhyncha might indicate that they still lived on the conifers like their archescytinid ancestors. The group I families other than Archescytinidae were confined to Subangara and marginal Angaraland and might be chiefly associated with conifers as well.

A very interesting find from Kureika (Tunguska Basin) is an ignotalid forewing with uniquely lobate-dentate apical margin, in opinion of A.V. Gomankov (pers. comm.) quite resembling the lobate margin of the leaves in some peltasperms (*Tatarina* spp. from the Vyatkian and post-Vyatkian deposits, including the species from the Tunguska Basin: Meyen and Gomankov, 1980; Gomankov and Meyen, 1986). It is one of a few presumed cases of Paleozoic leaf crypsis (see also Jarzembowski, 1994) and provides evidence of an association with peltasperms. Similar trophic relations are probable also for pereboriids, but some other members of the worldwide distributed family Ignotalidae could have fed on different large-leafed plants (other pteridospems?).

Synchrony of the peltasperm invasion and the mass penetration of Homoptera into the Siberian Region imply that at least some groups of Prosboloidea common for this phytochory and Subangara were associated with these plants. On the other hand, presence of the endemic prosboloid genera in both phytochoria indicates that the members of this superfamily lived on the other gymnosperms as well. Prosbolidae, the most diverse family of the Permian Auchenorrhyncha known in both hemispheres, should had possessed very diverse trophic relations; at least some of the derived prosbolid genera known in the Tunguska Basin might live on cordaites. An association with Peltaspermales is supposed also for Protopsyllidiidae, abundant up to the Jurassic but becoming extremely rare in the Cretaceous (Klimaszewski, 1995).

Scytinopteroidea most probably lived on helophytes and other hygrophilous plants, probably not only on sphenophytes (colonization of these latter being doubtless secondary). Helophytes and the plant communities adapted to flooding were more widespread and diverse in the Late Paleozoic than today (Ponomarenko 1996).

It is not surprising that the P-T extinction of arboreous vegetation, especially conifers (at least in Europe of all their Permian families: Visscher *et al.*, 1996),

resulted in the decline or transformation of many Permian homopteran groups (except for Scytinopteroidea). An association with ginkgophytes (descendants of peltasperms) has been assumed for Palaeontinidae, one of the dominant Mesozoic families, consisting of large, cryptically colored cicadas (Becker-Migdisova, 1960a). Possibly the extinction of this and some other lineages descending from Prosboloidea was correlated with the decline of most ginkgophytes by the end of the Mesophytic.

PERMO-TRIASSIC TRANSITION

Many symptoms of the ecological crisis (Kalandadze and Rautian, 1993; Barskov *et al.*, 1996) can be exemplified by the changes in hemipteran faunas about the P-T boundary. Before the crisis (in the Tatarian) the appearance rate of families increased, and then (to the end of the Permian) the differences between regional faunas were reduced. At about the time of the P-T boundary nearly half of the families became extinct, and many new ones originated, including some such as Ignotalidae that were widespread but short-lived. Key ecological innovations appeared, represented in the taxa dominating the Mid- to Late Triassic or even the all Mesozoic faunas: Hylicelloidea, the first Clypeata to adopt xylem-feeding, and possibly subterranean root-sucking at the nymphal stage (Shcherbakov, 1996); true bugs (Heteroptera), the first zoophages and first truly aquatic forms among Hemiptera (scytinopteroids, even if capable of submergence, were connected to shore plants). The number of extant taxa increased, their rank being lowered: in the Triassic the first living families of Hemiptera appear (Tettigarctidae, Naucoridae, Belostomatidae, Notonectidae). Some taxa were replaced by their descendants (dominant Hylicellidae instead of dominant Prosbolidae, Curvicubitidae instead of Pereboriidae). Highly specialized taxa became extinct (Coleoscytidae), including all the large cicadas (Pereboriidae, Ignotalidae, Prosbolidae). Before their final extinction phylogenetic relics (archaic forms persisting in marginal biotopes) became more common and widespread (Archescytinidae, Ingruidae). Some taxa, previously rare, became dominant (Dysmorphoptilidae, Dunstaniidae, Progonocimicidae), sometimes only for a short time before the crisis (Protopsyllidiidae, abundant only since the Jurassic). As judged from the Middle Triassic hemipterofaunas being impoverished relative to the Late Permian and Late Triassic ones, unknown Early Triassic faunas should be even poorer and consist mainly or entirely of Permian survivors. The faunal change was complete (no fauna of a mixed type is known). The post-crisis hemipterofaunas were relatively short-lived, being replaced from the end of the Triassic by fauna of the Meso-Cenozoic type.

At the P-T boundary latitudinal zonality was markedly reduced and the barriers separating biochoria vanished (on the land, and in the sea). In the floras (like in HFs) the former inhabitants of high latitudes of Anga-raland were replaced by immigrants from the lower latitudes, including those from the tropics; migration towards the poles was recorded in other zones as well (Zechsteinian conifer species in Nedubrovo: Krassilov *et al.*, 1999). Decrease in provinciality of the land faunas began earlier, as indicated e.g., by the tetrapods of Gondwanian origin reaching Europe (Ochev and Shishkin, 1998; Ochev, 1999). About the P-T boundary some species of non-marine invertebrates with bipolar (maybe even worldwide) distribution appeared (Conchostraca: Novozhilov, 1970). Ammonoids, at the end of the Permian known only from the tropics of the Paleotethys (Leonova, 1999), are recorded at the temperate latitudes as well from the beginning of the Early Triassic, their regional faunas differing only at the species level (Shevyrev, 1990); the widespread otoceratids marking the base of the Triassic section descended from the ancestors confined to the Dzhulfian and Dorashamian of the Paleotethys (Shevyrev, 1999).

In the P-T crisis Hemiptera changed in many respects analogous to the other non-marine groups: land plants (Meyen, 1987), tetrapods (Ochev and Shishkin, 1998) and beetles (Ponomarenko and Sukatsheva, 1998). Highly specialized and large forms were the first to die out, such as the trees (Visscher *et al.*, 1996) and pareiasaurs, and these vacant niches were subsequently occupied by unrelated taxa (Palaeontinoidea instead of Pereborioidea). With the fall of biogeographic barriers the inhabitants of the lower latitudes shifted to the higher ones (possibly escaping from extreme aridization of the tropics), and aquatic or amphibiotic groups (some of them short-lived or miniaturized) became widespread: Pleuromeiaceae, Lystrosauridae, Tupilakosauridae, schizophoroid Coleoptera (schiza on the elytra of these latter was used to lock the air in the subelytral space, just as the knob latch in scytinopteroids). Scytinopteroidea lost none of their four families in the P-T extinction (unlike the other homopteran superfamilies represented by more than one family in the Permian), and Scytinopteridae retained their dominance into the Triassic (unlike the other Permian dominants of Group II, Prosbolidae, having not crossed the P-T boundary). This success of the small, waterside scytinopteroids was a prerequisite for the origin and the great Mesozoic expansion of their descendants, Heteroptera, initially zoophages in the littoral zone and on the floating plant carpets, subsequently conquering various biotopes.

Even the advocates of an endogenous nature of biotic crises agree that the global synchronization of extinction events cannot be explained without exogenous factors (Barskov *et al.*, 1996). In the history of the Earth mass extinctions correlate with the flood basalt volcanic episodes having occurred quasi-periodically (Rampino and Stothers, 1988), and the largest eruption in the Phanerozoic record, the Siberian Traps at the P-T boundary, was associated with the greatest extinction (Campbell *et al.*, 1992). The P-T extinction was the

most profound for marine as well as for non-marine taxa, including the insects (Alekseev *et al.*, in press).

The Late Permian was a time interval with exceptionally widespread volcanism succeeding the assembly of the Pangea (Visscher *et al.*, 1996). This supercontinent which had already formed by the Early Permian became exposed during the end-Permian regression (Erwin, 1994). A possible mechanism of this regression and subsequent rapid transgression after the P-T boundary is a plume rising through the mantle and causing an uplift of the Earth's surface (at horizontal scale about 3000 km), so a considerable fraction of Pangea could have been lifted by some 50 m, and then dropped with eruption of the flood basalts (Renne *et al.*, 1995). Sometimes the formation of globally uniform and interconnected biota is regarded as an important prerequisite for a biotic crisis (historic-biogeographic "pangea:" Barskov *et al.*, 1996), though the barriers for spreading could be of the opposite nature for different groups, and disappear at the different time. The Late Permian regressions, resulting in the decrease of isolated sea basins and connection of the land masses, reduced the provinciality of the marine and tetrapod faunas, whereas the nearly complete elimination of latitudinal climatic zones which entailed the long distance migrations of the land plants and animals could be triggered by catastrophic volcanism at the P-T boundary. One can try to trace the common tectonic grounds (and even deeper ones, e.g., changing parameters of the Earth's rotation) under these changes in the sea level and climate, same as under the flood basalt episodes.

The scale of the P-T crisis seems to be especially large because of the transition from cryo- to thermoera, when the high latitude climate became far warmer and the low latitude one drier, presumably due to an alternative type of circulation in the ocean (haline instead of thermal) and in the atmosphere (meridional prevailing over latitudinal: Chamberlin, 1906; A.G. Ponomarenko, pers. comm.). Such a circulation is consistent with developed sectoral differentiation and reduced latitudinal zonality of Eurasian floras in the Mid- to Late Triassic (Dobruskina, 1982).

The P–T crisis gave rise to an impoverished and at the global scale more homogenous Early Triassic land biota with lycopods and conifers dominating the flora (Retallack 1995), resetting life on earth back to the simpler ecosystems; coal deposition was interrupted until the Mid-Triassic due to extinction of the peat-forming plants (cordaites, glossopterids, etc.: Retallack *et al.*, 1996). The high atmospheric oxygen level characteristic of the Late Paleozoic had dropped abruptly because of the burial of unoxidized organic matter stopped on the land (Ponomarenko, 1993) and in the ocean, and due to extensive oxidation of the organic matter in the ocean (Gruszczyński *et al.*, 1989). The climate and land biota were probably the most affected by several factors resulting from catastrophic volcanism: rapid sea level changes, acid rain, short volcanic winter followed by greenhouse conditions, anoxia (Bowring *et al.*, 1998), excessive ultraviolet radiation (due to destruction of the ozone layer: Krassilov *et al.*, 1999). Anoxia and ultraviolet radiation might cause the preferential extinction of larger forms and miniaturization in various phyletic lineages. With the disappearance of forests, protection from harmful ultraviolet could be achieved by submergence in water wring the day.

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