

## MATERIALS TO THE TETRAPOD HISTORY AT THE PALEOZOIC-MESOZOIC BOUNDARY

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#### 1. On the relationship between the history of Triassic tetrapods from Eastern Europe and climate evolution\*

A number of successive tetrapod associations, from the late Permian through the Middle Triassic ones, is known from Eastern Europe (Ochev & Shishkin, 1989) (*Fig. 1.1*). One can trace the relationship between their change with time and climatic changes through the end of the Permian and during the Triassic. This may be achieved by means of group composition analysis. Such type of analysis is especially important in case of the Early Triassic tetrapod associations from Eastern Europe, which are the most representing ones among those known from the arid belts of that time.

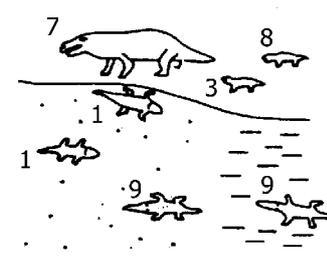
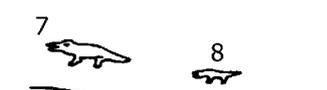
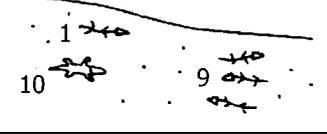
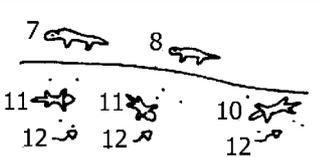
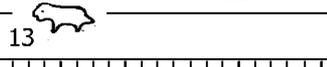
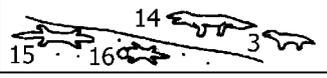
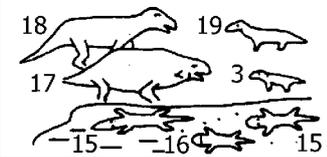
The following statements might form the basis for interpretation. 1) Therapsid predomination according to Robinson in more humid settings and that of sauropsids in more arid ones. Charig (1984) criticized the

soundness of the actualistic approach which had been fundamental for Robinson's conclusion. But the conclusion itself is confirmed by biogeographic reconstruction for the Early Triassic (Ochev, 1993); 2) It was easier for small ancient tetrapods to find favorable living conditions in arid climate than for larger ones; 3) The most arid settings are characterized by poor associations of terrestrial animals, but if permanent reservoirs are available, relatively diverse aquatic animals exist.

The Early Triassic stage in the tetrapod history in Eastern Europe is distinguished for labyrinthodont predominance and for an appreciable role of ancient archosaurs among reptiles. The oldest tetrapod find from that stage, a semiaquatic anomodont *Lystrosawus georgeii* Kaland., was made by G. I. Blom within the base of the Triassic — in the only point of the Astashihian subsuite, on the Vetluga river (Lozovsky, 1983). The first one of extensive Triassic vertebrate associations is fixed to the Vokhminian horizon. Labyrinthodonts constitute the dominant group there: *Tupilakosaurus* and others. Procolophonids and lepidosaur remains are common among those of small reptiles. On the contrary, early archosaurs, proterosuchians, are rarely found, though their size was equally small. *Lystrosaur* (?) fragments

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I	II	III	IV	V	VI	VII		
T <sub>2</sub>	Bukobaj series	Mastodonsaurus fauna		4	7	arid. hum.		
	Donguz series	Eryosuchus fauna		4-5	15			
T <sub>1</sub>	Yarenian horizon	Parotosuchus fauna		6	13-15			
	Vetlugian superhorizon	Neorhachitomosus fauna	Sludkian horizon	Wetlugasaurus			6-7	6-7
			Rybinskian horizon	Benthosuchus			4-5	5-6
			Vokhmian horizon	Tupilakosaurus			4	7
			Astashikhinian subseries	Lystrosaurus				1
P <sub>2</sub>	Vyatkian horizon	Archosaurus-bearing complex		2	>3			
		Pareiasaur-gorgonopsian complex		6	10			

**Fig. 1.1.** Changing tetrapod complexes at the Paleozoic/Mesozoic boundary in the Cis-Urals: I — general scale; II — regional stratigraphic units; III-IV — tetrapod complexes; V-VI — number of animal genera (data on the Vyatkian horizon from G.I. Iverdokhlebova; the number range reflects different views on systematics); V — amphibians; VI — terrestrial; VII — climatic curve (arid — aridization; hum — humidization); 1 — capitosauroids; 2 — plagiosaurs; 3 — theriodonts; 4 — rhaeusuchids; 5 — euparkeriids; 6 — kannemeieroids; 7 — proterosuchians; 8 — procolophons and protolizards; 9 — trematosaurids; 10 — benthosuchids; 11 — lidekkerinids; 12 — tupilakosaur; 13 — lystrosaur; 14 — archosaurus; 15 — batrachosaurs; 16 — dvinosaur; 17 — pareiasaurs; 18 — gorgonopsians; 19 — dicynodon.

were found at the above mentioned *Lystrosaurus* site on the Vetluga river, higher across the section within the base of the Vokhminian horizon — along with *Tupilakosaurus*. Small theriodonts could have been absent from the burial-site due to their rarity. Mass material counting has shown that labyrinthodonts amounted 90% and terrestrial reptiles — about 10% of finds in the Vokhminian deposits. The latter figure is of course affected by taphonomic information loss. Such a marked difference testifies to domination of vertebrate biomass in basins.

Some features of the Vokhminian tetrapod association are indicative of its existence in sufficiently arid conditions. 1. The majority of terrestrial animals were peculiar for very small size. 2. Ecological niches for large terrestrial herbivores and predators were vacant. This may be explained, however, by the fact that evolution hasn't yet produced any new large-sized animals after the extinction of such forms at the end of the Permian. Nevertheless, *Chasmatosaurus*, a proterosuchian known from South Africa and China, from the lowermost Triassic corresponding to less arid settings, might be as large as 1,5–2 m. 3. Theropsids (especially anomodont *Lystrosaurus*) that were rather important in the Early Triassic faunas of Antarctic, South Africa, India and China, were evidently rare in the Vokhminian association. *Lystrosaurus* dominated there over a significant part of the Early Triassic. But this genus was uncommon in Eastern Europe and apparently disappeared rapidly as early as during the Vokhminian. It has been mentioned already, that theropsids represented by theriodonts and anomodonts were less adapted to arid conditions than sauropsids-lepidosaurs and archosaurs. It is substantial climate aridity that might provide a logical explanation for lystrosaur historic fate in Eastern Europe. 4. Only aquatic adaptations were characteristic of labyrinthodonts which is probably indicative of terrestrial conditions being unfavorable to them.

The Vokhminian association seems to have existed under the conditions of seasonal

climate with protracted droughts. Major river streams and lacustrine basins, though, were hardly ever drying up completely. This would be at variance with the abundance of labyrinthodonts which were far from being small-sized.

We believe the Vokhminian vertebrate association to have existed under more arid conditions than the preceding Late Permian pareiasaur group — the gorgonopsian one. This is indicated by the importance of large, obviously semiaquatic pareiasaurs within the latter group, and by sufficient variety of land-inhabiting theriodonts.

Many changes in vertebrate fauna at the boundary of the Tatarian and the Vetluzhian may be accounted for from the position of climate aridization. Large herbivores (pareiasaurs) and large predators (gorgonopsians) die out. The former are completely gone already, the latter ones are extremely rare in the latest (Sennikov, 1988). Tatarian association containing the *Archosaurus rassicus* Tat. proterosuchian, which is possibly related to progressive aridization that has begun at the end of Permian. General reduction of theriodont number by the end of the Triassic has the same ecological sense. Spreading protero-suchians were taking their places then among small predators. The Vokhminian proterosuchians were substantially smaller than *Archosaurus*. It is reasonable to speculate that the Vokhminian aridization has prevented any further development of large terrestrial animals even among the then existing archosaurs. On the contrary, small terrestrial animals procolophones and various lepidosaurs — not so dependent upon climatic variations, proceeded on their autochthonous development as well as small proterosuchians. It was not just climate alone that controlled the fate of those groups, but its role was very important.

The majority of East European reptiles at the boundary of the Paleozoic and Mesozoic were evolving autochthonously. But breaking ecosystem relations following the extinction of the Permian groups made wide spreading possible for a short period of time. It was then that almost worldwide distribu-

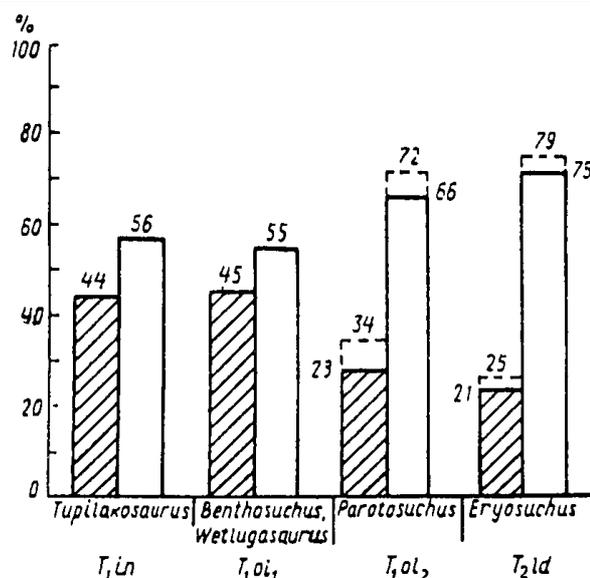
tion of *Lystrosaurus*, originating probably from South Africa, occurred. As it has been mentioned earlier, however, its existence in Eastern Europe proved to be a short-timed episode. Among labyrinthodonts, Capitosauridae and Benthosuchidae were evolving autochthonously. Since the beginning of the Triassic, Lydekkerinidae have spread globally from South–Eastern Gondwana, and *Tupilakosaurus* — from the northern margins of the latter (Shishkin & Ochev, 1993).

Aridization maximum was associated with the Vokhminian. This is indicated by the analysis of tetrapod association from the Rybinskian and Sludkinian horizons, still close to the Vokhminian association. *Benthosuchus* labyrinthodont represents the dominant for the Rybinskian and *Wetlugosaurus* — for the Sludkinian. A new benthosuchid subfamily appears here: Thoosuchinae, procolophones with differentiated dentition. The number of finds and diversity of early archosaurs increase, according to Sennikov, rauisuchids appear. Proterosushians (*Chasmatosaurus*) become large in size and by the end of the Sludkinian some of them reach the size of the small specimens of their descendants, *Garjainia*, which are to spread later on. Scarce theriodonts are represented by a Rybinskian genus *Scalopognathus*.

Evolution of *Chasmatosuchus* towards growing size was probably associated with reducing climate aridity degree. The environment might be suitable enough for relatively large terrestrial animals. But the seasonal climate of that time was characterized by still long-termed dry periods compared to the regions of development of mainly theropsid faunas. The ecological niches for any large herbivores and predators in Eastern Europe were still vacant. The development of the vertebrate fauna at the Vokhminian/Rybinskian boundary was mostly autochthonous. Wide distributions might be prevented by climatic barriers.

More marked humidization associated with certain changes in vertebrate fauna is recognized at the beginning of Jarenian (Fig. 1.2).

Within the Jarenian association, among labyrinthodonts, the larger *Parotosuchus*



**Fig. 1.2.** Histograms relating the numbers of amphibian (oblique hatching) and reptilian genera for various faunas in the east of the European part of the country. Dashed lines reflect different views upon systematics.

replaces its ancestor, *Wetengasaurus*; Trematosauridae replace Thoosuchinae in a similar manner. The most ancient representatives of Plagiosauridae (Melanopeltd) appear as well as Brachiopidae — immigrants from Gondwana (Shishkin & Ochev, 1993). Among the terrestrial reptiles, archosaurs are represented by *Garjainia* genus, descending from *Chasmatosuchus*: those were the first large (up to 3 meters long) predators in the whole of the Early Triassic history of Eastern Europe. A number of smaller forms also exist; A. G. Sennikov regards the majority of them as rauisuchids. Further indeterminate proterosaur remains are also distinguished for larger size than in the preceding associations. Procolophone diversity becomes rather large. Scarce trilophosaurs and theriodonts are known.

Many researchers wrote about the more humid Jarenian climate compared to that of the Vetluzhian; their conclusions were based on the important role of grey-coloured sandstone deposits. Decreasing aridity seems to have made evolution able to produce the type of large predators represented by *Gar-*

*jainia*. Improving conditions for life on the land are indicated by the increase of other animals' sizes and by general diversity of terrestrial life. While the Vetluzhian terrestrial reptiles excel amphibians in the number of genera but slightly, the number of reptile genera in the Jarenian is twice larger. Rather large sizes and various adaptations of labyrinthodonts indicate reservoir expansion. Various types of passive (Brachiopidae, Capitosauridae) and active aquatic predators (Trematosauridae) are known from there.

The Jarenian climate may be possibly regarded as variable humid to subarid. But judging from extreme scarcity of synapsids in the Jarenian association, it is less humid than that in the regions of therapsid faunas development. According to I. A. Dobruskina, the occurrence of arid settings in Eastern Europe is indicated by the finds of the Voltzian flora in the Petropavlovskian suite from the South Cis-Urals. Autochthonous development was evidently the main process in formation of Jarenian vertebrate association.

The boundary between the Early and Middle Triassic in Eastern Europe can't be studied because the data are incomplete. The differences between the Jarenian and stratigraphically higher association of the Donguzian suite are, however, in some respects representative as resulting from environmental changes. Labyrinthodont sizes have increased substantially by the Middle Triassic all over the world. Similar faunas were distributed in all the regions with the environmental conditions acceptable for large reptiles. Their abundance, especially quantitative, in the Donguzian association (capitosaurid *Eryosuchus*, plagiosaurids) is indicative of large reservoirs available there. Diverse terrestrial fauna, comprising some rather large animals, testifies to improving life conditions on the land. The role of therapsids, associated with more humid settings, increases: of theriodonts and, what is more humid important, of anomodonts — Kannemeyeroidea. Relatively scant arid vegetation of Early Triassic in Eastern Europe couldn't provide any sufficient forage for large her-

bivores. On the contrary, scitophyllic flora of the time concerned, lacking any features of marked aridity, according to Dobruskina, seemed to provide it. The younger Bukobanian vertebrate association is characterized by the same climatic setting as the preceding one.

Everything mentioned above testifies to humidity increase by the Middle Triassic. Some taphonomic features of certain localities, however, point to the occurrence of dry seasons: dried up channels, turbidity currents peculiar of arid areas. Thus, we get a picture of a less arid, but seasonal climate.

A number of groups among these in the Middle Triassic associations seem to have evolved autochthonously in Eastern Europe: labyrinthodonts, procolophonids, archosaurs. Kannemeyeroidea that appeared in many regions of the world at the end of the Early- at the beginning of the Middle Triassic, don't demonstrate any obvious roots in the East European Early Triassic. They have most probably disseminated from Gondwana, when migration ways were opened with weakening climatic differentiation of the Early Triassic. The same may prove true for certain theriodont groups.

Any younger tetrapod associations from Eastern Europe are unknown.

Thus, the relationship is revealed between the evolution changes of the terrestrial tetrapod fauna, particularly of its group composition, at the Paleozoic-Mesozoic boundary, and climate aridization that began as early as at the end of the Permian. The aridity maximum falls at the beginning of the Triassic: the Vokhminian time.

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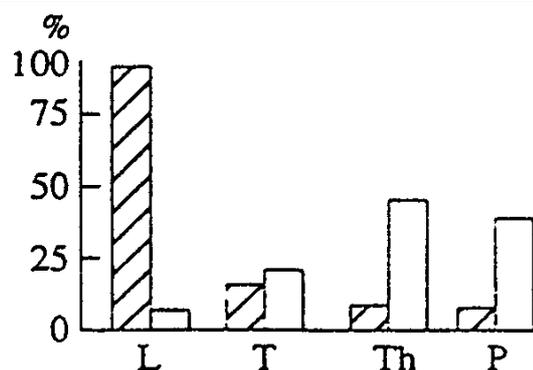
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## 2. On the Peculiarities of the Early Triassic Ecosystems of South Africa and the Fore-Urals\*

The theme of this paper is central to the study of tetrapod evolution at the Paleozoic-Mesozoic boundary, i. e. the richest Early Triassic localities: the Listrosaurian Zone of South Africa and its stratigraphic equivalents in the Fore-Urals — the Wetlugian Superhorizon of the Indian-Early Olenekian age (according to the latest correlation given in Shishkin, 1995). I compare only the reptilian components of these communities. In addition to considerable generic endemism, they also differ in their higher order taxa that are even more dissimilar than in both the earlier, Permian, and the later, Middle Triassic faunas that contain abundant kanemeyeroids.

Some differences of the South African and Fore-Uralian assemblages are shown in the histogram (*Fig. 2.1*) depicting relative frequencies of the main reptilian groups. Its most important features are: (1) an extreme scarcity of *Listrosaurus* remains in the Fore-Urals (two occurrences in the basal Triassic of the Wetluga River Basin); (2) the low diversity of the Fore-Uralian theriodonts (a single genus against six to nine genera in South Africa); (3) the obviously higher taxonomic diversity of the Fore-Uralian thec-



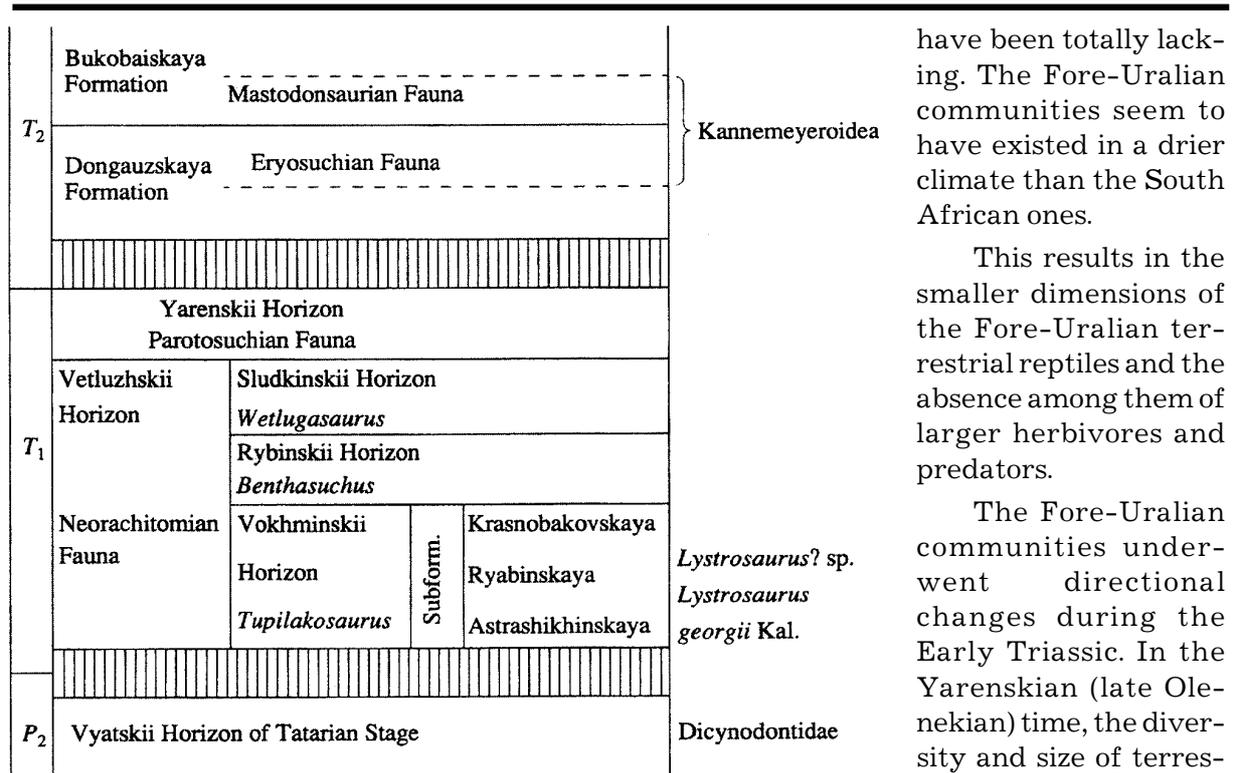
**Fig. 2.1.** Ratios of the different reptile groups in the Listrosaurian zone of South Africa (stippled) and the Wetlugian of the Fore-Urals: L — Lysirosaundae, T — Theriodontia, Th — Thecodontia, P — Procolophomidae and other small reptiles.

odonts (five genera against one or two in South Africa), procolophonids (eight genera against two or three) and other small reptiles; (4) small size of the terrestrial Fore-Uralian reptiles that became larger only toward the end of the Early Triassic; (5) vacancy of ecological niches of large herbivores and predators in the Fore-Urals during the larger part of the epoch (there were no ecological links between the early disappearing listrosaurs and the late appearing large proterosaurs).

It has to be mentioned, in addition to the above listed differences, that in the Fore-Urals, almost lacking therapsids, there was a sole brief listrosaurian event (*Fig. 2.2*) in contrast to the long-lasting listrosaur-dominated stage encompassing the whole Listrosaurian zone of South Africa. This has to be kept in mind in discussing the Wetlugian finds of *Listrosaurus*.

The rest of the known Early Triassic communities are less diverse and are divisible into two types: the therapsid (listrosaurian) and the essentially non-therapsid. It was noted that the former are confined to the middle and high paleolatitudes while the latter are more common in the lower paleolatitudes (Ochev, 1992, 1993, 1994; Shishkin, 1995). These occurrences seem to indicate climatic control. However, temperature control (Yin Hong-Fu, 1989) appears improb-

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**Fig. 2.2.** Stratigraphic occurrences of dicynodonts in the Fore-Urals (also indicated are two finds of listrosaurids in the basal Triassic).

able, since in the Triassic, lacking polar glaciations, temperature gradients had to be rather gentle. Another explanation (Ochev, 1993, 1994) relates to a well known hypothesis advanced by Robinson (1971) that for therapsids, as representatives of therapsids, arid conditions were less favorable than for sauropsids, the difference being due to peculiarities of nitrogen metabolism in the latter. This hypothesis was refuted by Charig (1985). He argued that phylogenetic affinities are not indicative of similar nitrogen metabolism, thus giving no evidence of metabolism type in Triassic tetrapods. I do not wish to engage in this physiological discussion. Logical, however, if tetrapod biogeography was climatically controlled, than perhaps there were physiological differences between various groups of these animals. This assumption seems compatible with some auxiliary data. In present day Earth, arid zones occur in the low latitudes, with a humid zone between them. In the Triassic, however, the global climate was much more and, and the humid equatorial belt might

have been totally lacking. The Fore-Uralian communities seem to have existed in a drier climate than the South African ones.

This results in the smaller dimensions of the Fore-Uralian terrestrial reptiles and the absence among them of larger herbivores and predators.

The Fore-Uralian communities underwent directional changes during the Early Triassic. In the Yarenskian (late Olenekian) time, the diversity and size of terrestrial reptiles increased while in the Middle Triassic there was a rise of therapsids, and the

larger herbivores appeared. This may indicate an amelioration of Triassic climate (Ochev, 1992, 1994). Coal accumulation in the Middle Triassic and, on a larger scale, in the Late Triassic, indicates a global extent of humid belts. Certainly, the above mentioned changes of tetrapod communities reflect normal evolutionary progression after the end-Permian mass extinction. However, the evolutionary patterns, as well as regional peculiarities, might have been controlled by climatic conditions. For instance, the middle-sized herbivores and carnivores, still lacking in the Wetlugian communities, already appeared in the concomitant listrosaurian community where they were represented by listrosaurids as well as by Chasmatosaurus (based on the skull series described by Cruikshank).

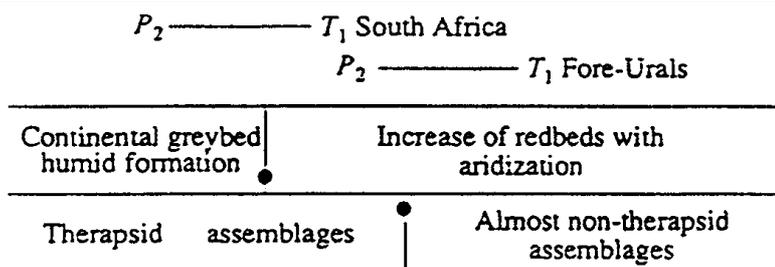
Thus we still face considerable difficulties in assessing tetrapod ecology in a more systematic way, taking into consideration the lithologies of the localities and the associated plant assemblages. In general, the Triassic faunas of Eurasia and South Africa are

more distinct than the corresponding Late Permian faunas uniformly dominated by therapsids. However, the Upper Beaufortian (Lower to Middle Triassic) aleuropelitic redbeds are more similar to the contemporary Fore-Uralian redbeds than the grey deposits of the Lower Beaufortian (late Permian) to their stratigraphic equivalents in the Fore-Urals. One can assume that the so-called «arid redbeds» might actually have been formed under

a wide range of seasonal climates. Judging by the Late Permian tetrapod communities of South Africa and the Fore-Urals, the dominant groups remained similar in both the humid depositional environments of greybeds and in the, to a certain extent seasonal, redbed environments, diverging under considerably increased aridity alone (Fig. 2.3). In other words, environmental changes that are most obviously reflected in the lithologies of the tetrapod-bearing beds seem significantly different from those affecting tetrapod communities in the first place (see fig. 2.3.).

The floristic evidence is likewise uncertain. In the Fore-Uralian, Triassic plant localities are confined to the Olenekian deposits. According to Dobruskina (1982), they contain the poorly preserved pleuromeian and voltzian assemblages that are considered as sufficiently xerophilic. Their climatological comparison with the earlier tatarinian and the later *Scitophyllum* floras is as yet not provided by paleobotanists. I have attempted such comparisons on the basis of tetrapod communities.

In Gondwanaland, the late Paleozoic glossopterid flora was replaced by the more xerophilic early Triassic dicroidian flora. This floristic change is usually related to climatic deterioration in Listrosaurian time. Andersen and Andersen (1993), however, found no definite plant macrofossils in the Listrosaurian zone while palynological data indicate conifer forests, Pleuromeia and



**Fig. 2.3.** Correlations of the climatically defined lithological types and tetrapod communities in the Upper Permian, Lower Triassic and Middle Triassic. Black circles show the divergence of lithological and faunistic indicators in relation to the Permian-Triassic boundary positions in South Africa and the Fore-Urals.

horsetail «meadows». These authors consider the floristic transition poorly documented and enigmatic. We can only assume that climatic conditions indicated by the fossil plants remained in the adaptive range of the therapsid faunas.

As for climatic interpretation of the Early Triassic floras, I am aware only of Grauvogel-Stamm's (cited in Blicek et al., 1988), that recognized three floristic realms, the Gondwana, the Angarian (with the stratigraphic equivalents of Listrosaurian fauna), and the Eurosinian, indicating arid climatic conditions for the latter alone. This conclusion agrees well with my assessments based on the tetrapod faunas. Other paleobotanists, however, refrain from definite climatic evaluations.

To conclude, I consider the above causal scheme of tetrapod differentiation as a working hypothesis. Obviously, South Africa and the Fore-Urals are the most promising areas for the study of terrestrial tetrapod environments and of the role played by the alternation of humid and arid climates in their evolution.

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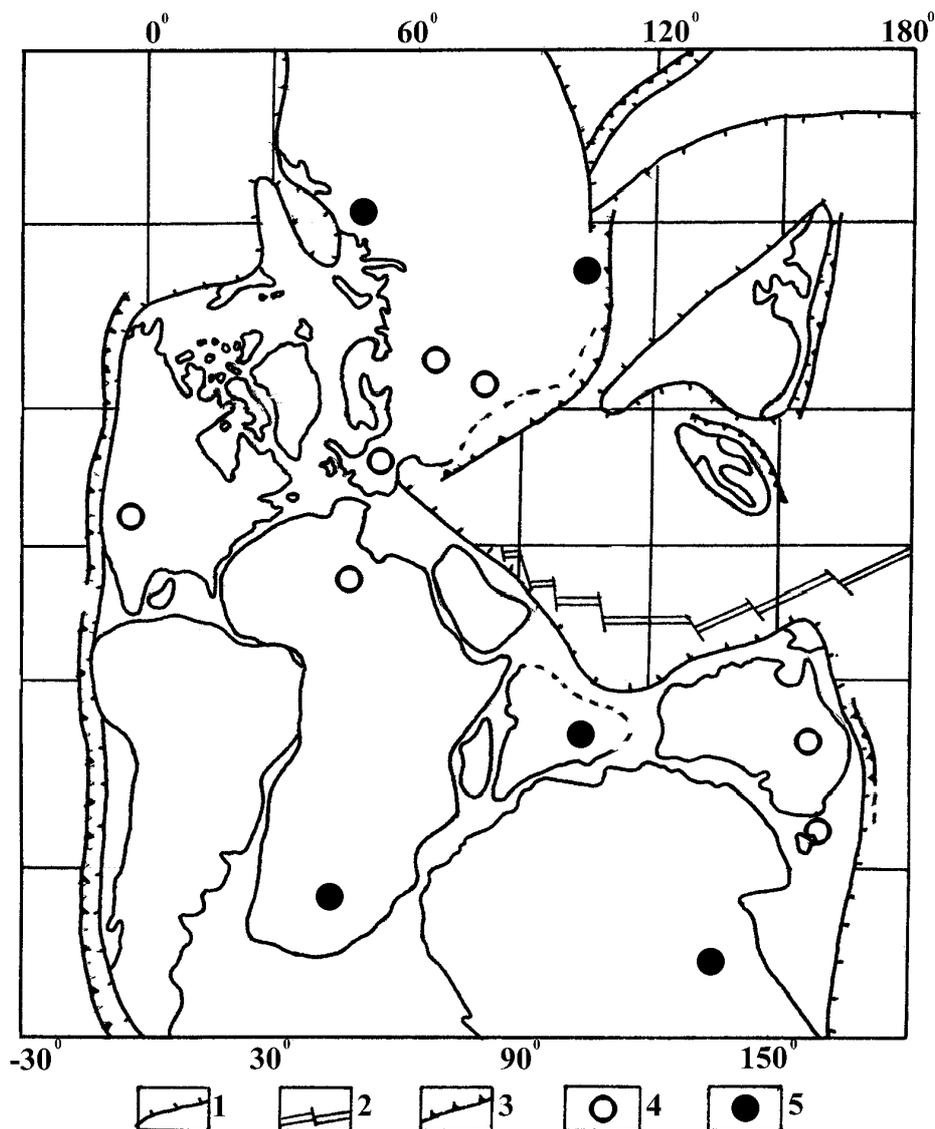
### 3. To the comparison among the regional faunas of the Euramerian Triassic tetrapods

In the Early Triassic, the Euramerian biogeographic region (Fig. 3.1) was situated in the north-west of a vast arid belt hosting faunas almost devoid of therapsids (Ochev, 1993). The most complete record of tetrapods from that region is encountered in the fluvial beds from Eastern Europe: *Tupilakosaurus* associations (Induan) — *Benthosuchus* and *Wetlugasaurus* (Early Olenekian) — *Pa-*

*rotosuchus* (Late Olenekian), named after the most characteristic labyrinthodont genera (Shishkin & Ochev, 1993). In the Lower Buntsandstein from Germany, basin deposits infavourable for concentrations of tetrapod remains are of considerable importance (Ochev & Tverdokhlebova, 1997). Growing throughout the Early Triassic amounts of channel-lag deposits have resulted in more frequent tetrapod finds in Hardeggen Formation, whence, in particular, labyrinthodonts came to be known, similar to the Late Olenekian ones from Eastern Europe (*Parotosuchus*, *Trematosaurus*). No tetrapod finds come from the Lower Triassic of Great Britain, represented mainly by too coarse clastic deposits. In other, more westward areas of the Euramerian region, the section of the continental Triassic being incomplete (at least the Induan and the Lower Olenekian are missing), only the following labyrinthodonts are known: the Late Olenekian *Wellesaurus* (descending from *Wetlugasaurus*) from North America and the Early Anisian *Eocyclotosaurus* (descending from benthosuchians) found in North America, northern Africa and Germany.

The above data on the Early Triassic tetrapod faunas from the central and western areas of the Euramerian region are incomplete due to taphonomic reasons and stratigraphic gaps. The situation may be partially improved on the basis of the following assumptions. 1. The early East-European capitosaurids and trematosaurids, ancestral to the above mentioned later genera (*Wellesaurus* and *Eocyclotosaurus*) penetrated into the western areas of the region as well. 2. In the Induan, *Lystrosaurus* anomodonts, labyrinthodonts — *Tupilakosaurus* brachiopoids and Lydekkerinids (*Luzocephalus*) — might have incidentally arrived in Eastern Europe from Gondwana through North Africa and West Europe, with short-term dwelling of those settlers there.

West Europe was located during Triassic in the central part of the north arid belt. Because of high degrees of aridity western European early Triassic labirintodonts were yielded by sizes to close related forms from East Europe (*Parotosushus*, *Trematosaurus*)



**Fig. 3.1.** Distributions in the Early Triassic of almost thersapsidless tetrapod faunas, associated with arid climates, and of thersapsid faunas, associated with less arid climates (Pangea reconstruction for the end of the Permian according to Khain, Soslavinsky, 1991). 1 — boundaries of the continental crust regions; 2 — spreading axes and transform faults; 3 — subduction zones; 4 — almost thersapsidless tetrapod faunas; 5 — thersapsid tetrapod faunas.

Distribution of large dicynodonts within the Middle Triassic thersapsid faunas from the non-arid regions significantly affected only Eastern Europe, lying in the margin of the arid belt; this was associated with increasing humidization.

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#### **4. Ancient therapsid communities and biomes\***

Pangean tetrapod faunas at the end of the Permian and the beginning of the Triassic, were very monotonous in the superfamily range groups. However, within the empire of continental lowlands, two types of communities may be recognized, associated with different climatic belts. They differ in the dominating groups: one community Scarce therapsids (probably preferring humid conditions contrary to diapsids) and domination of reservoir residents. The other one Therapsid abundance and consequent significance of terrestrial life. At the end of the Permian, the most complete communities of the first type are known from Eastern Europe and Brazil: domination of amphibians, pareiasaurs feeding on soft vegetation, prevalence of xerophilous flora. These are associated with the northern and southern arid-semiarid belts. Communities of the second type are well represented in South and East Africa: domination of various terrestrial therapsids, especially dicynodonts, and facies similarity of host deposits with those from Eastern Europe (plains subjected to wide flooding). Scarcity of amphibians there is unaccountable at present. The climate of that period varies from warm, humid to semi-arid. At the beginning of the Triassic, communities of the first type were common in Eastern Europe and Australia; amphibians dominated and terrestrial life was poor due to therapsid scarcity and still small diversity of diapsids. These were related with a vast low-latitude extra-arid belt. It is clearly distinguished in the background of general aridization from lithologic data. Communities of the second type are known from higher latitudes: from South Africa and India, less complete ones from north China and Siberia. Semi-aquatic and terrestrial therapsids play significant part. The Late Permian Brazilian and Early Triassic Australian

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\*from: Abstracts VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires, 1999. P. 47.

faunas are closer to the typically Gondwanan South African one is historic — genetic respect; as far as the community type is concerned, they are closer to the Euramerian East European one. Both types of communities represent biomes of the epochs considered.

#### **5. Rich faunas of the ancient tetrapods that used to exist in transitional climatic settings\*\***

Tropical and subtropical temperature conditions were dominant over vast areas in the Late Permian and Triassic. Similar belts of the present epoch comprise the following climatic sequence of the landscape-geographic zones, based on the degrees of humidity: constantly moist forests — seasonally moist, light (monsoon) forests — forest-savannahs — humid savannahs — arid savannahs, tropical and subtropical steppes — desertified savannahs, semideserts — deserts. Various researchers associate forest savannahs, humid and arid savannahs and, frequently, semideserts with transitional (semihumid — semiarid) climates. Large terrestrial animals (absent in the constantly humid forests rich in crown-dwellers) become abundant among the vertebrates starting from the sparse forest and forest-savannah settings. Such features of the fauna that becomes just somewhat poorer systematically, are maintained to involve the settings of arid savannahs and steppes. An important part is played by reptiles and amphibians, some of them hibernating. The animal world is highly impoverished in taxa and individuals in semideserts and desertified savannahs (Grigoryev, 1970).

Rich faunas of large Late Permian and Triassic tetrapods are generally associated with arid (carbonate) red-bed formations. Paleontologists frequently regard such fau-

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\*\* from: Abstracts book «VI European Workshop on Vertebrate Palaeontology», Firenze-Montevarchi, Italy, 19-22 September 2001, 2001: 43.

na habitats as humid, while lithologists consider them to be arid. The actualistic data above, testify to the rightfulness of a compromise conclusion: that of living in transitional, as regards humidity, settings. Distinguishing between the semihumid and semi-arid paleosettings, is complicated by diverse views on distinguishing between modern climates. Many Russian climatologists and landscape specialists associate semiaridity with steppes and dry savannahs, some of them extend the notion to semideserts. Still other scientists, mostly from the West, confine semiaridity to semideserts. Adhering to the first point of view, we may assess the habitats of the Early Beaufort tetrapods from South Africa as mostly semihumid, and those of poorer Tatarian faunas from Russia — as mostly semiarid.

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## 6. Climatobiogeography and tetrapods from the Permian-Triassic Pangea\*

Life evolution at the Paleozoic/Mesozoic boundary makes an important chapter in the history of life. Those events were associated with global climatic changes. This makes study of climatobiogeographic evolution a key aspect for their understanding. We face a number of problems related to the object of our analyses — ancient terrestrial vertebrates.

The first one — formation conditions of the Upper Permian and Triassic tetrapod-remains-bearing sequences generally known as «arid red beds». In the paleogeographic reconstructions available, the problem of aridity degree is a matter of dispute between lithologists and paleontologists. So-

lution lies in accepting the fact that the deposits called «arid red beds», might form in the conditions corresponding to seasonal climates with rather wide range of humidity. The resulting settings may often be of mosaic character: permanent basins may neighbour caliche formation (e. g. Behrenmeyer et al., 1979). Those settings varied in time. The paleoclimatic gradations for the range mentioned above, like monsoon-semiarid-arid, have but conventional limits. It is more real to recognize wider characteristics for the historic stages analyzed here: humid to semi-arid, semiarid to arid, etc.

The second problem — the probable ways of reconstructing climatobiogeography for ancient tetrapods. The methods for community classification and zoning were developed most intensively in phytocoenology. Of the approaches applied there, the «physiognomic» one provides the most clear association with climate; this approach is based on consideration of dominants and life forms. The approach has led to the ideas of biomes. Similar physiognomic features of communities may be traced in compositions of fossil faunas, of ancient tetrapods in particular, called forth by a complex of historic and ecologic reasons.

In searching for such criteria, it is most interesting to use P. Robinson's theory (Robinson, 1971) on the relations between climate aridization in transition from the Paleozoic to the Mesozoic and the change of therapsid domination (therapsid for the time considered), their imperfect water exchange, domination of sauropsids, more perfect in this respect (archosaurs, lepidosaurs). This hypothesis was criticized (Bonaparte, 1982), but it has not been ruined by other independent data related to the Permian-Triassic transition (Ochev, 1996b). P. Robinson revealed the relationship between the communities and the climate (*Fig. 6.1*), and used this relationship to analyze the events in time. We use these ideas for biogeographic reconstructions, but on the basis of peculiarities of the beds hosting tetrapod remains, we intend to associate therapsid communities to wider ranges of climates, seasonal as regards dis-

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\*from: Bull. Moscow Soc. of Naturalists. Geological section, 2000. Vol. 75. Part. 5. P. 4246

Climate Tetrapods	Arid and semiarid	Musonnian and savannahian	Constantly humid and warm
Amphibians		—	
Sauropsids	—		
Theropsids		—	

**Fig. 6.1.** Distribution of ancient tetrapods in different climate conditions, from Robinson, 1971.

tribution of precipitations; besides, we have different views on the role of amphibians (Ochev, 1994). The climatic criteria accepted here, may be formulated as follows.

During the period of therapsid domination on the dry land and still insufficient role of sauropsids (i. e. from the Permian to the Middle Triassic), growing aridization should have been manifested by great impoverishment of tetrapod fauna in representatives of terrestrial adaptations (principally large forms) and increasing relative numbers (percent number of specimens) of the representatives associated with water reservoirs. This is true within the areas of seasonal climate development, with permanent water basins. The most arid of such settings might be characterized by the faunas dominated by amphibians, with an unimportant role of large reptiles (particularly herbivorous). The tetrapod communities of the settings beyond the areas of substantial permanent water basins were, probably low in number and are not reliably identified in the paleontologic record of that time.

While using the above mentioned criterion for biogeography, it is quite natural to operate life settings similar in other respects. These are vast lowland plains accumulating fluvial and lacustrine formations hosting remains of rich tetrapod faunas; they were formed in diverse climatic conditions: in humid settings — the resulting sequences are grey-coloured, occasionally coal-bearing, and in more arid conditions — the deposits are red and carbonate-bearing there. Other tetrapod complexes, bearing little similarity with the previous ones, may be associated with vast intracontinental water basins and peculiar local settings. Such complexes (e.g. Andersen & Cruickshank, 1978) are not included in the present comparison.

Temperature gradients have reduced with glaciopause disappearance by the beginning of the Mesozoic, and as early as in the Early Triassic, tetrapods have spread to the circumpolar regions. It is impossible to reveal any definite temperature influence in the assemblage peculiarities.

Spreading of all ancient tetrapod faunas was limited only by ice settings. There are more prospects for analyzing climate aridity or humidity degrees.

Ancient tetrapod features important for climatobiogeography are peculiar mainly of large taxonomic groups, generally widely spread geographically. That is why the biogeographic reconstructions based upon such features may reflect historic-genetic relationships in a generalized way. Such relationships are most completely reflected in zonation of those ancient faunas at the levels of families, partly, of genera. Any break between the paleoclimatic and historic-genetic approaches would have reduced the historic value of biogeographic reconstructions. Thus, it is reasonable to make an attempt of synthesizing the reconstructions based on the above community peculiarities and on the fauna family compositions. This presents still another problem.

N. A. Bobrinsky (1959) noted that in current zoogeography, primary division of the global land is based not on the ecologic differences, like in the World ocean representing a whole water area, but on the differences stipulated by the historic unity of individual faunas associated with the continents separated in various periods long ago. Within the continents, on the contrary, the ecologic (first of all, climatic) conditions are of primary importance for animal spreading. Existence of a whole supercontinent, Pangea, made the transitory stage between the Paleozoic and the Mesozoic absolutely unique. It may be proposed, that with the end of Pangea formation, the ecologic differences determining the historic-genetic differences as well, might have become the principal basis for the biogeographic divi-

sions of both, the joint land area and of the oceans. This would have provided opportunity for recognizing tetrapod biochores isolated both, ecologically and historically, similar to I. Schmitzhuzen's plant divisions (Shmitkhuzen, 1966). The experience of developing tetrapod biogeography for the Permian-Triassic Pangea, shows, that this coincidence is but partial. This may be associated with the earlier history, with the enormous area (Zonenshain et al., 1984; Scotese & McKerrow, 1990) of the supercontinent, with complicated configuration. We attempted to combine both approaches, attributing the leading role to the historic-genetic one, but aiming at uttermost disclosing of the biogeographic role of paleoclimate. This has resulted in reconstructions, not completely unequivocal logically, but useful for historic studies.

The transitory period in tetrapod history between the Paleozoic and the Mesozoic, when therapsid domination was substituted with sauropsid prevalence, lasted almost for the whole of the Triassic. We attempted biogeographic reconstructions with all the above mentioned aspects in mind for the very end of the Permian (Ochev & Surkov, 1996), for the Early and the Middle Triassic (Ochev, 1994a).

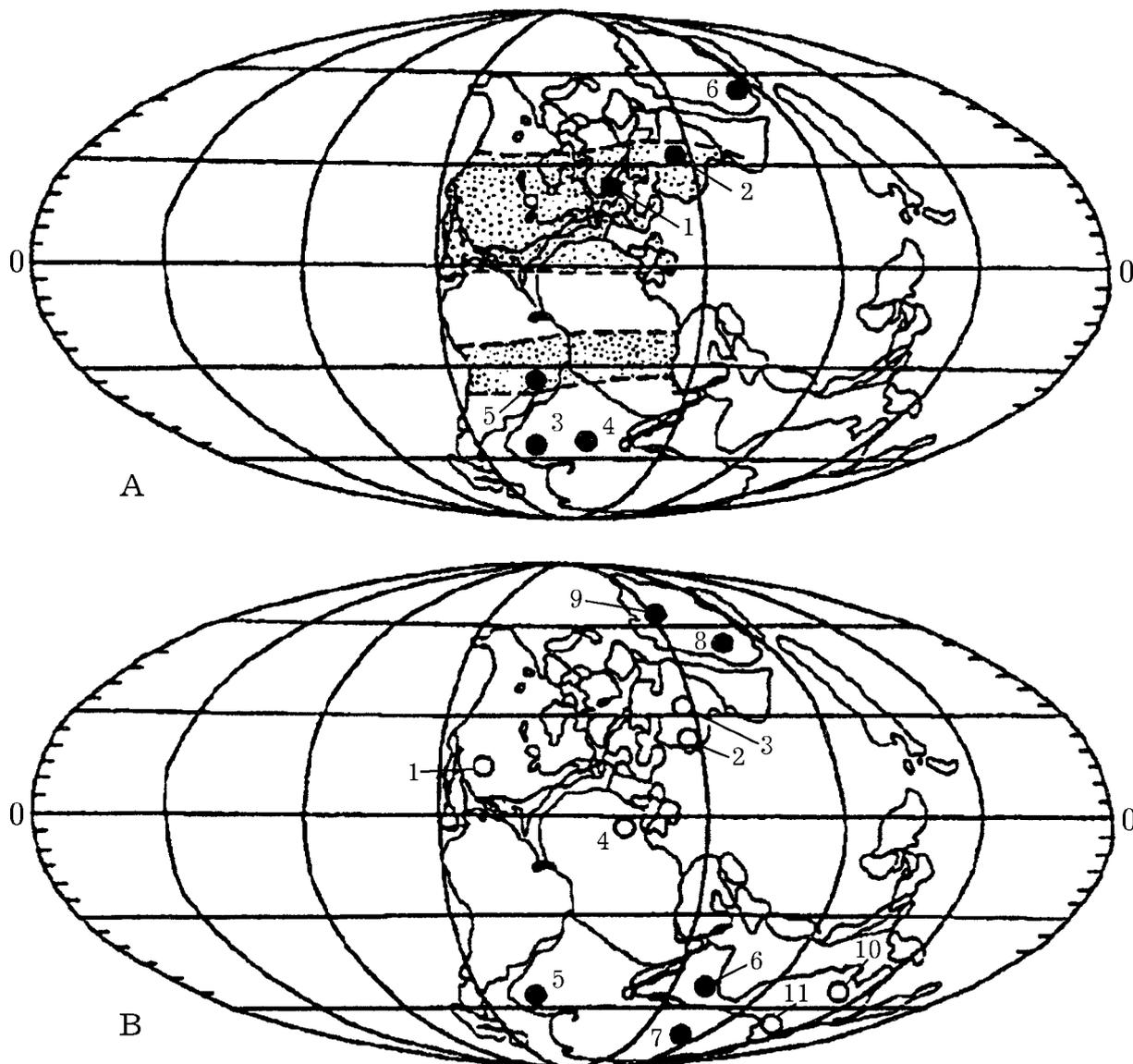
In the end of the Permian, faunas with high therapsid diversity were, probably, common all over the world (except the circumpolar areas) and formed the Therapsid Gea (*Fig. 6.2, A*) which was accounted for by wide development of favourable climate conditions. Though the regions with fairly rich tetrapod faunas are not numerous, two different areas may be recognized against the general background. The fauna from one of them is well represented in the red beds from the uppermost Tatarian stage in East Europe, being, thus, associated with the northern arid belt, lithologically outlined by N. A. Yasamanov (1985). The fauna from the other area is most typically represented in South Africa, in the uppermost of the Lower Beaufort — mainly in the grey-coloured and even coal-bearing beds, i. e. beds that have clearly been formed in more humid

conditions. We believe, that due to the paleoclimate differences in the periods of the host-deposit formation, compositions of those fossil faunas may bear differences associated with the peculiarities of the communities inhabiting the areas mentioned. High percentage of amphibians in the East European fauna, compared to the number of terrestrial animals, is a natural sequence of the more favourable living conditions in water in a fairly xerophile climate. The occurrence percentage of amphibian remains is unexpectedly low in the South African fauna from the more humid environment.

This results either from omitting fragmentary material from consideration, or from the still unexplained rarity paradox» of amphibians in the reptiles-rich Permian-Triassic tetrapod faunas of the Gondwana type; this paradox is manifested in China. The most meaningful physiognomic difference of the faunas from the areas considered, lies in domination of terrestrial therapsids, dicynodonts, in South Africa, and domination of parareptiles, pareiasaurs, feeding on soft vegetable food and being inclined to water reservoirs, in East Europe; reduction of the systematic diversity of terrestrial animals was peculiar for East Europe, as well.

The East European fauna differs from the South African one historically-genetically — in abundance of anthracosaurs and Seymouriamorphs, that after the Early Carboniferous kept on developing only in Laurasia, and in certain peculiarity at the family level. The data on tetrapods of this period from the more westward areas are incontinuous and incomplete. Having in mind, however, that that was the time of ultimate Pangea shaping and of general regression, it seems but natural to suppose that the area considered occupied, most probably, the whole of the northern arid belt, and may be called Euramerian. It should be pointed out, that the ecologic peculiarities of the dominant groups there testify to the important role of semiarid conditions in that belt.

There is no sufficient information on tetrapods from many Gondwana regions up to the very end of the Permian. Judging from



**Fig. 6.2.** Distribution of terapsid (black circles) and demon/nearly off-terapsid (white circles) faunas of ancient tetrapods. A — Terapsid Geya at the end of Permian: 1-2 — Euroamerian area (1 — Scotland, 2 — East Europe); 3-6 — Gondwanian area: 3-4 — Central Gondwanian subregion (3 — South Africa, 4 — East Africa), 5 — Brazilian subregion, 6 — Sinian subregion. Dotted line — arid belts, based on lithological data; from N. A. Yasamanov [II]. B — a breakup of Terapsid Geya in early Triassic: 1-4 — Euroamerian area (1 — Arizona, 2 — West Europe, 3 — East Europe, 4 — Algiers); 5-11 — Gondwanian area: 5-9 — Central Gondwanian subregion (5 — South Africa, 6 — India, 7 — Antarctica, 8 — North China, 9 — Noril'sk), 10-11 — Australian subregion (10 — Queensland, 11 — Tasmania). Extraarid belt on the background of general aridization, based on lithological data, was not traced. Pangean model from Scotese and McKerrrow, 1990.

the facts known of their family and generic compositions, especially from Brazil and China, the faunas of the whole of Gondwana and of China may be historically-genetically referred to the united Gondwana region, as it was accepted by N. N. Kalandadze

and A. S. Rautian (1981, 1983). The dominating communities, tetrapods included, were, however, different within the area. South and East Africa, with the above mentioned features of tetrapods living in humid conditions, may be regarded as the Central Gond-

wana subregion. In Brazil, within the south arid belt outlined by N. A. Yasamanov from lithologic data, alongside with the peculiar glossopterian flora (Rohn and Rosler, 1989) of arid habit, a tetrapod fauna is known, «physiognomically» similar to the East European one (Barberena & Araujo, 1974) — domination of amphibians and pareiasaurs, small number of terrestrial synapsidans. Though this fauna is older than the terminal one from the Dicynodon zone in the Permian of Gondwana, the tendency to general aridization by the end of the Permian allows to suppose that tetrapod population of the region had similar features in later time, as well. Considering the historic-genetic similarity of the Brazilian and the South African faunas, we recognize just the Brazilian subregion there — due to the ecologic peculiarities mentioned above. China, with the fauna historically-genetically somewhat closer to the Gondwanan one, and ecologically transitory, may be conventionally recognized as the Sinian region. There is no reliable data on Permian tetrapods from Siberia. The combination of the historical-genetical and the climatobiogeographic approaches has resulted in non-unequivocal reconstructions: regions have been recognized on historical and paleoclimatic grounds, subregions — on the latter one only.

Comparing the Early Triassic tetrapod faunas, we may notice that some of them (the East European and the Australian ones) are characterized by extremely unimportant role of therapsids. The vast belt of highly arid climate, that has formed by that time, broke the Therapsid Gea (*Fig. 2.6, B*). The Euramerian sector of that belt, occupying the north-western part of Gondwana, broader than in the Permian, as well, was isolated from the eastern sector, the Australian one, due to complicated Pangea outlines. The first one, with almost therapsidless fauna (principally labyrinthodont-archosaur fauna), best represented in East Europe, may be regarded as the Early Triassic Euramerian region. That region was historically-genetically different from the Gondwanan one, occupying the rest of the above mentioned southern

continent; the difference is best manifested in rich and well-studied amphibians (Shishkin & Ochev, 1993). To maintain the principle accepted for the Permian, the Australian therapsidless fauna, physiognomically very similar to the Euramerian one, but historically-genetically close to the fauna from less arid Central Gondwana, should be recognized just as a subregion of the Gondwana region. China is the northernmost known area of therapsid (lystrosaur) fauna in the Central Gondwana subregion; this might be reached across Tethys, through a chain of microcontinents — across «Battay's bridge» (Kalandadze & Rautian, 1983). There is too little data on the more northern analogues of lystrosaur faunas found in Siberia.

The Late Triassic climate is considered to be extremely contrasting in space and time, but judging from intensified coal formation in high latitudes, generally this has become more humid. Evaporite spreading in low latitudes may be associated with origination of numerous embayments resulting from growing transgressions. The Carnian age was probably peculiar for continuation of the Ladinian humidization followed by the Norian aridization (Simms & Rufell, 1989). As early as in the Carnian, however, and thus, without any association with the climate evolution, therapsids lose the leading role in tetrapod communities everywhere. The latest known fauna with therapsids prevailing over archosaurs and large dicynodonts occurring commonly, comes from the lower part of the Ishigualasto formation (Lower Carnian) in Argentina (Bonaparte, 1982). With the disappearing faunas represented mainly by large therapsids, potentials of the above considered way of climatobiogeographic reconstructions become exhausted. Climatic peculiarities, however, might have influenced therapsid spreading even in the Late Triassic (Robinson, 1971).

On the whole, the Late Triassic epoch, with dominating sauropsid representatives — archosaurs peculiar for larger ecologic potentials — demonstrates great similarity of the regional faunas. This results in the «faunal Pangea» (Kalandadze & Rautian,

1983) or Diapsid Gea coming into being. Climatic differences may be reflected in archosaur peculiarities. Thus, R. E. Kirby (1993) links aridization with disappearance of large herbivorous thecodonts from the upper member of the Petrified Forest-Owl Rock formation in Arizona. One might make an attempt to consider this feature during spatial analysis, but the current factual data is far from being enough. Regarding the Late Triassic, the problem of metaposaur and phytosaur absence from South Africa and South America is the one considered most often; this may not be related with climate peculiarities.

Our attempt to combine the faunal historic-genetic biogeography and the climatobiogeography of ancient tetrapod communities in Pangea has led to obtaining the results that are not completely, but to a certain degree similar. Focusing on the biogeographic role of paleoclimates is essential for understanding the history of life. Thus, the problems of the role of competition in therapsid substitution by archosaurs at the Paleozoic/Mesozoic boundary, or the problem of global extinction of large herbivorous parareptiles, pareiasaurs, by the end of the Permian can't be solved without taking into account the peculiarities of the events in various climate belts. It is reasonable to point out, that on the way to the completely causal historic-genetic paleobogeography, climatobiogeographic reconstructions make a necessary preliminary stage.

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