

On Traces of Non-Equilibrium States in the Evolution of Terrestrial Vertebrate Communities across the Paleozoic–Mesozoic Boundary

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Received November 17, 2020; revised March 31, 2021; accepted March 31, 2021

Abstract—Evolutionary change in a living system starts with a disturbance to its equilibrium and an increase in its internal disorderliness. Typical manifestations of this process are exemplified by the transformation of the tetrapod faunas across the Permian–Triassic boundary. These are seen both at the end of the transition to a new equilibrium (in the pioneer Triassic faunas) and at its beginning (in the terminal Permian communities). In the first case, the most distinct manifestations are: unfinished state of structural changes within some new groups; a high degree of endemism of regional pioneer communities, and the heterogeneity of their change with time. In the second case, as can be seen from analysis of the early-crisis (Vyaznikovian) biota of Eastern Europe, the observed events primarily include the “precocious” appearance of some future dominants; the “return” of a number of relics to the fossil record; and examples of explosive group variability in some taxa close to extinction. Actual or probable traces of non-equilibrium changes, similar to those noted in the Vyaznikovian biota, can also be partly traced in other Late Permian faunas of Eurasia and in coeval communities of southern and northern Gondwana.

Keywords: Permian, Triassic, tetrapod faunas, evolution, organizational equilibrium, disorderliness

DOI: 10.1134/S0031030122010117

INTRODUCTION

The transition of any system to a qualitatively different equilibrium state begins as a decrease in the effective regulation of its parameters under threshold conditions. Their fluctuations, caused by growing external disturbances, become more and more long-term (i.e., their relaxation slows down) and eventually turn into irreversible changes. This disturbance means a loss of balance by the system and, accordingly, a decrease in its orderliness. This course of events underlies, in particular, biological evolution (Spencer, 1899; Volkenstein, 1984), regardless of whether phyletic or biotic changes are concerned, because all of them begin with the *loss of the previous equilibrium of a living system*.

In the first of these cases, the disturbance of the orderliness of the typical organization of taxa at the species or group level is concerned. Its initial decline (in successive cycles of ontogenesis or on a historical time scale) manifests itself as the replacement of the previous organizational norm with an increasingly wider range of its unstable deviations; i.e., it means an increase in the scope of its variability (Shishkin, 2015, 2018, 2019a). The selection for enhancement of the most viable variations leads to the emergence on their

basis of mosaic (and mostly short-lived) types of organization, grotesquely combining features of its previous appearance with certain features of a new equilibrium model, in the direction of which the evolutionary search is going (not necessarily successfully implemented). When applied to the characteristics of these early alternative lines arising in the course of formation of such a new model, this phenomenon was called “archaic diversity” (Mamkaev, 1968). On the other hand, its very earliest stages of manifestation, recorded even against a background of the predominance of features of initial organization, are known as “racial senescence” (Hyatt, 1866), or an increase in phylum variability at the eve of extinction (Simpson, 1953), or as terminal instability (Shishkin, 2015).

Another above-mentioned aspect of the assessment of an evolutionary event as a transition to a new equilibrium concerns the rearrangement of the organization of an entire biota. The patterns associated with this process are most evident at large-scale ecosystem changes. Among the signs of a decrease in orderliness during such a transition, one of the most expected ones is a drastic heterogeneity (local endemism) of the emerging pioneer post-crisis communities. In this case, the disturbance or disintegration of coenotic

relationships that controlled the previous state of the biota opens the way for a rapid emergence of new dominants. The latter may include both groups or forms that are not known in the previous geological record and those that were considered to have disappeared much earlier. A characteristic feature of these not fully established communities is a significant role of ephemeral components (dominant or other) with a short time of existence. A general analysis of the history of such regional communities usually also reveals other aspects of their heterogeneity in terms of both the stages of events recorded in them and the duration of this history itself (Shishkin et al., 2006; Shishkin, 2018b, 2019b).

**PIONEER FAUNAS OF THE EARLY TRIASSIC
AS A RESULT OF THE DISORDERLINESS
OF EVOLUTIONARY PROCESSES
CAUSED BY THE CRISIS
OF THE LATE PERMIAN BIOTA**

All of the above can be demonstrated by the example of the transformation of the world of terrestrial vertebrates at the boundary of the Permian and Triassic, corresponding to the epoch of the largest planetary ecosystem turnover. The direct result of this event in the form of the most ancient (Induan–Early Olenekian) tetrapod faunas of the Early Triassic, known in a number of variants on almost all continents, is most available for analysis. In the most studied faunal sequences that are usually used for planetary correlations, this time interval generally corresponds to the interval of the *Tupilakosaurus*–*Wetlugasaurus* faunas in Eastern Europe and the *Lystrosaurus* Zone in South Africa (Ochev and Shishkin, 1989; Shishkin and Ochev, 1993; Shishkin et al., 1995). In addition to these two regional biotas, the faunas of Australia–Tasmania and South America are also the most significant for the purposes of our consideration. In the cases listed above, the history of early post-crisis communities allows establishing for them one or another stage of events or, at least, their temporal heterogeneity. In this case, the main material for assessment is the information on the change in temnospondyl amphibians, because they either completely dominated or played one of the main roles in the majority of communities of that time (except for South Africa and Antarctica).

*Organizational Instability
of Early Triassic Pioneer Groups*

Traces of disorderliness of the structural organization are retained in several early families of Triassic temnospondyl amphibians. In general, the Mesozoic Temnospondyli, with all the differences in their modes of life, constitute a rather morphologically homogeneous evolutionary grade. Its main feature is the “stereospondyl” consolidated cranial structure, which

obviously represented the optimal type of organization in a purely aquatic environment typical of late Temnospondyli (Shishkin, 2018a, 2019a)¹. Since the Middle Triassic, there are no exceptions in the versatility of this construction; i.e., the observed variations are within its scope. However, within the early Triassic pioneer families, it does not always look complete; that is, the “stereospondyl” body plan can be combined here with the mosaic of individual features of more ancient (Paleozoic) morphotypes. This combination of characters of *different evolutionary levels*, found at the level of low-rank taxa, is, as already mentioned, a typical feature of archaic diversity.

One of such examples of structural disorderliness among pioneer Triassic amphibians is Tupilakosauridae, an aberrant family of trimerorachomorph Temnospondyli. Against the background of the predominance of the features of the “stereospondyl” organization in them, they usually retain some ancient features unexpected for the Mesozoic forms, such as the dominance of the basioccipital in the occipital joint and the exposure of the carotid arteries on the palatine surface of the skull (Shishkin, 1973; Warren, 1999). However, it is noteworthy that the transition from these relict features to conditions typical of Triassic temnospondyls also took place *within* this family (i.e., independently from other groups), which was documented as a rare deviation at the generic level (Australian form described as *Brachyopoidea* indet.; Damiani and Warren, 1996; cf. Shishkin, 2019a).

Another example of an incomplete transition to a new (Mesozoic) model of organization relates to retaining the archaic structure of the coronoid series of the lower jaw in some early Triassic groups of amphibians. In this case, the precoronoid is in wide contact with the symphyseal plate of the dentary and constitutes its posterior continuation. Thus, the conditions typical for Devonian protetrapods (cf. Ahlberg and Clack, 1998) are retained; however, they are already rare even among the early temnospondyls (Shishkin, 1994; Shishkin and Sulej, 2009). This picture is common for the pioneer early Triassic family Rhytidosteidae (genera *Arcadia*, *Rhytidosteus*, and *Mahavisaurus* (Warren and Black, 1985; Shishkin, 1994; Maganuco et al., 2014)). The same is also known for a number of Gondwanan lydekkerinids (*Lydekkerina*, *Chomatobatrachus* (Cosgriff, 1974; Hewison, 2007)). However, the only their Laurasian representative *Luzocephalus* had already achieved the condition that is normal for temnospondyls (i.e., the symphyseal plate and the precoronoid are separated and lie in different planes (author’s observations)). Thus, in this case, as in tupilakosaurids, the transition

¹ The stability of this construction essentially underlies the prevailing cladistic ideas about the monophyly of “stereospondyls” (Shishkin, 2018a, 2019a).

to the “Mesozoic” type of organization proceeded independently. Similar processes were observed in the early evolution of the dominant group of Triassic amphibians, the superfamily Capitosauroidae. In its oldest (early Scythian) subfamily Selenocarinae, in contrast to all other “stereospondyls,” the rudimentary state of the retroarticular process of the lower jaw, resembling the conditions in the Paleozoic forms, is retained (Novikov, 2016).

All this evidence of the internal heterogeneity of individual temnospondyl groups in terms of the degree of completeness of their transition to a new (Mesozoic) organizational equilibrium corresponds to the expected patterns of systemic transformation (see above). Apparently, this process was also heterogeneous in those Triassic groups of Temnospondyli for which the geological record did not preserve its documented early traces.

Heterogeneity of the Composition and Pathways of Transformation of Local Biotas

The pioneer regional communities of Triassic tetrapods exhibit a high heterogeneity of composition expressed in their generic endemism (which often complicates their age correlation). Only single taxa with short episodes of explosive spatial distribution (against the background of the disunity of local biotas) are sometimes revealed as an exception. In these early faunas, reptiles were very scarce (with an exception of South Africa, Antarctica, and partly China), both in terms of diversity and frequency of occurrence. Their most common groups for the Induan time include, in particular, parareptiles-procolophonids, which were represented on different continents by local genera with unicuspid teeth and, in most cases (except for Eastern Europe), were documented by only rare records (Cisneros, 2008a). The transition to bicuspid teeth in the early Olenekian time (which apparently occurred simultaneously in several lineages) was marked in South Gondwana by an episode of expansion of the genus *Procolophon* in South Africa, Antarctica, and South America (Cisneros, 2008a, 2008b; Dias-da-Silva et al., 2017; Peacock et al., 2019). A characteristic element of the early Triassic faunas are also diapsids archosauromorphs (primarily pseudosuchian proterosuchids). In most cases, the latter are known only from fragmentary remains, which complicates the assessment of the validity of the distinguished taxa and the nature of their relationships. Among their Induan representatives, only the close relationship of the South African *Proterosuchus* from the base of *Lystrosaurus* Zone with the Chinese “*Chasmatosaurus*” (“*Ch.*” *yuani*) from the Jikayuan Formation seems rather obvious (Ezcurra, 2016). For the early Olenekian Stage of the early Triassic history of tetrapods, reliable information about proterosuchids is

apparently limited to the data on *Chasmatosuchus* from Eastern Europe².

The pattern of distribution of therapsid reptiles, which dominate the faunas of South Africa and Antarctica but are usually poorly known on other continents, seems to be the most heterogeneous for the beginning of the early Triassic. The only exception to this background is the episode of the expansion of the dicynodont *Lystrosaurus*, which invaded part of the Gondwana subcontinents, Northern Asia, and, to a minimum extent, Eastern Europe (Fröbisch, 2009).

Unlike amniotes, temnospondyl amphibians are more or less widely represented in almost all Induan faunas, forming highly endemic communities within them. These communities are formed by a small group of mostly short-lived families, the majority of which arose at the transition between the Permian and Triassic. About half of them are known in the Induan time almost exclusively in the Southern Gondwana subcontinents either everywhere (Lydekkerinidae and, probably, Rhytidosteidae) or only in Australia–Tasmania (Brachyopidae)³. Conversely, in Laurasia, lydekkerinids were represented at this time by the only local genus, whereas rhytidosteids (rare endemic forms) first appeared only in the early Olenekian (Shishkin, 1980; Shishkin and Vavilov, 1985). True brachyopids, apparently, did not occur here at all during the Triassic (Shishkin, 2011). On the other hand, primitive trematosauroid families (Benthosuchidae and Thoosuchidae), which belong to the dominants of the early Scythian fauna of Eastern Europe, are entirely endemic to Laurasia.

The most cosmopolitan amphibian family in the Induan communities is Tupilakosauridae with independent genera, at least in Europe (Shishkin, 1973, 2011), South Africa (Warren, 1999), and Australia (Damiani and Warren, 1996; Shishkin, 2019a). Another rather common component is the oldest lineages of the superfamily Capitosauroidae, the dominant Triassic group that undoubtedly evolved in parallel in Laurasia and Gondwana (Watson, 1962; Ochev, 1966; Shishkin et al., 2004). The earliest representatives of these independent lineages are, respectively, the European subfamily Selenocarinae and Australian forms such as *Rewanobatrachus* (Shishkin et al., 2006; Novikov, 2016, 2018; cf. Schoch and Milner, 2000).

² However, the recent assessment of the relationship of *Chasmatosuchus* places it in the aggregate (polytomy) of difficultly positioned taxa, “intermediate” between proterosuchids and erythrosuchids (Ezcurra, 2016). The same situation is accepted for the Antarctic genus *Antarctanax*, which is apparently younger than the South African *Proterosuchus* (Peacock et al., 2019). The coeval Tasmanian genus *Tasmaniosaurus*, which is usually classified with proterosuchids, in these analyzes is regarded as a sister taxon to Archosauriformes.

³ Examination by the author in 1993 of the specimen from the Lower Fremouw Formation (basal lower Triassic) of Antarctica, once classified as a brachyopid (Colbert and Cosgriff, 1974), did not confirm this conclusion (see also: Warren and Marsicano, 2000).

Another nominally common but, most likely, heterogeneous pioneer group includes Lonchorhynchinae trematosaurids. The relics of Paleozoic dominants (dissorhophoids and rhinesuchids) are reliably known in the beginning of the early Triassic only in South Africa.

Against a background of endemism of pioneer amphibian communities of the early Triassic, cases of a wider distribution of their individual genera are extremely rare. One such example is the only record of the South African *Lydekkerina* in Australia (Warren et al., 2006); information on the presence of this genus in India seems more problematic (cf. Tripathi, 1969; Shishkin et al., 1996; Schoch and Milner, 2000). It also cannot be ruled out that the Induan lonchorhynchinid *Gonioglyptus* penetrated Eastern Europe (Shishkin et al., 2006).

The stages of events in the short history of the pioneer tetrapod faunas of the Triassic (approximately covering the Induan–early Olenekian) also do not show homogeneity for different land blocks. An illustrative example is the comparison of the community of the South African *Lystrosaurus* Zone with its total equivalent in South America, i.e., with the faunas of the Buena Vista Formation (Uruguay)⁴ and Sanga do Cabral Formation (Brazil). Typical markers of two different-age intervals of the *Lystrosaurus* zone, namely, tupilakosaurids and primitive procolophonoids (in combination with lydekkerinids) at its base and, on the other hand, the abundance of the species *Procolophon trigoniceps* in its upper part are directly reflected in the Uruguayan fauna and in the upper distribution range of the Brazilian fauna, respectively (Píñeiro et al., 2004; Shishkin, 2009; Dias-da-Silva et al., 2017). However, the two above-mentioned South American communities are clearly separated and do not have taxa in common, whereas clear age divisions in the chronologically equivalent *Lystrosaurus* fauna cannot be distinguished, although its composition definitely changed with time (Shishkin, 2018b, 2019b).

The initial history of development of the Triassic tetrapod faunas of Australia–Tasmania is no less isolated. In this region, two types of pioneer communities are distinguished (Cosgriff, 1984)—the fauna of the Arcadia and Rewan Formations in eastern Australia and the fauna with the guide rhytidosteid genus *Deltasaurus*, represented in the Blina Formation (in the west of the continent) and Knocklofty Formation (in Tasmania). Although their dominants include members of a number of common amphibian families (primarily rhytidosteids and brachyopids), they do not show a clear evolutionary trend indicating their age sequence; for this reason, the latter is estimated primarily only indirectly. The age of the fauna of the

Arcadia Formation is identified as Induan based on the accompanying microflora, as well as by the presence of a putative tupilakosaurid and primitive procolophonoid (Warren et al., 2006; Shishkin, 2019a). The fauna of *Deltasaurus* is usually assigned to the early Olenekian (or Induan–early Olenekian) based on comparisons with coeval biota from the coastal marine sediments of the Kockatea Formation in the Perth Basin of Australia, which bear the ammonites and conodonts (Shishkin et al., 2006; Haig et al., 2015; cf. Berrell et al., 2020). No common taxa for these two pioneer faunas have been reliably established⁵.

A separate picture, difficult to compare with previous variants, is demonstrated by the early history of the Triassic tetrapods of Europe, which was documented in European Russia and partly in Greenland. In comparison with the Gondwanan faunal sequences, it is known in more detail and is relatively well dated due to the records of a number of the guide genera of amphibians in the coastal-marine sections (Ochev and Shishkin, 1989; Shishkin and Ochev, 1999; Shishkin et al., 2000). The Induan stage here includes two distinct successive episodes, which together belong to the *Tupilakosaurus* fauna (Shishkin and Novikov, 2017). The earliest of these corresponds to a depleted biota dominated by the genus *Tupilakosaurus* per se (in the absence of other temnospondyls, except for the lydekkerinid *Luzocephalus*). Late episode community, known only in the southeast of the East European Platform (in addition to single records in Greenland), shows a sharp increase in taxonomic diversity (Novikov, 2016, 2018). Among the new amphibians, the most typical members are the endemic European capitosauroids (Selenocarinae) and their derivatives (Syrtosuchinae), as well as the first Lonchorhynchinae and some “common” trematosauroids, fully or partly represented by local genera.

The early Olenekian stage in the evolution of Eastern European communities is spatially much more widely documented and also includes two main age intervals. They correspond to two faunas, the first of which is dominated by primitive trematosauroids, represented by typical Benthosuchidae, and the second is dominated by capitosauroids of the subfamily Wetlugasaurinae. Neither of these groups are known outside of Eurasia. They are also accompanied by the radiation of several non-bentosuchid trematosauroid lineages, primarily the endemic Thoosuchinae, as well as the poorly known family Quantasidae. A common feature of all the considered European communities (as well as later ones, up to the Ladinian time) is the pres-

⁴ The Uruguayan fauna is sometimes considered as transitional from the Permian to the Triassic (Píñeiro et al., 2003, 2015), based on imprecise identifications of some its components (cf. Shishkin, 2009; 2018b, 2019b).

⁵ At the same time, for their accompanying fishes, a common species of dipnoans, the ceratodontid *Ptychoceratodus phillipsi*, is reported (Kemp, 1996; Berrell et al., 2020). The latter is attributed to a wide age range, also covering the Middle Triassic of South Africa (where its holotype originates: Kemp, 1996) and the Carnian of Brazil, which may cast doubts about the accuracy of the species identification of the Australian records.

ence of rare relict anthracosauromorphs (Chroniosuchia) endemic to Eurasia (Shishkin et al., 2014).

All the above shows that the appearance of the most ancient tetrapod land faunas of the Triassic shows various signs of a non-equilibrium (disordered) state, which, apparently, characterized the transition from the Permian type of biota to the Early Mesozoic one. These signs include: (a) heterogeneity and incompleteness of structural changes in the organization of a number of recently emerged groups, (b) a high degree of endemism of pioneer regional communities, and (c) a heterogeneous picture of successions of the latter over time.

MANIFESTATIONS OF INSTABILITY OF THE TERMINAL LATE PERMIAN TETRAPOD FAUNA OF EASTERN EUROPE

The features of the pioneer communities of Triassic vertebrates considered above, indicating their incomplete stabilization, were the result of ecosystem rearrangement associated with the decay of the Late Permian terrestrial biota. Irreversible changes in the latter, associated with the loss of its systemic equilibrium, apparently proceeded relatively quickly, and episodes of their temporary stabilization in new changing conditions could not be long. Therefore, the probability of their traces being preserved in the geological record is generally low.

From this standpoint, the most documented and rare exception today is the Vyaznikovian vertebrate fauna of Eastern Europe, which corresponds to the terminal (late Vyatkian) time of the late Permian. This fauna, known mainly from the basin of the Klyazma River near Vyazniki and, in more patchy way further eastwards, up to the Volga–Vyatka interfluvium, was considered in many studies (for review, see Shishkin et al., 2018). Compared with the previous late Permian communities of the Sokolki type (Sennikov and Golubev, 2017), it shows characteristic manifestations of non-equilibrium (transitional) composition, which are indicative of the search for a new stable organization by the regional terrestrial biota. Among these manifestations, several main categories can be distinguished, which are discussed below.

Although in terms of group composition the Vyaznikovian community generally retains a late Permian appearance, its trophic organization changes towards a pattern characteristic of the Mesozoic. Large phytophagous pareiasaurs, together with gorgonopsian predators, which were on the top of the food pyramid in the faunas of the Sokolki assemblage, disappear here. Their role passes, respectively, to dicynodonts, and among predators to therocephals and the first proterosuchian archosaurs, represented here by their only Paleozoic genus *Archosaurus* (Sennikov and Golubev, 2006). The mentioned trophic relationship between dicynodonts and proterosuchids precedes its consoli-

dation already in the earliest history of the early Triassic biota of South Africa (Reig, 1970), where these groups are represented by the genera *Lystrosaurus* and *Proterosuchus*, respectively.

The appearance of archosaurs in the Vyaznikovian fauna, anticipating their dominance in the Mesozoic, is here only one of the examples of “precocious” formation of new historically stable types of organization triggered by the collapse of relationships within the late Permian biota. In the accompanying ichthyofauna, similar events include the first appearance of ceratodontiforms among dipnoans, as well as, possibly, saurichthyids among actinopterygians (Minikh et al., 2011, 2014; Lebedev et al., 2015).

Another similar distinction of the Vyaznikovian community from the previous late Tatarian faunas is associated with the appearance in it of relict anthracosaurs represented by chroniosuchians of the family Bystrowianidae. Although the latter were first recorded in the Middle Permian of China (Shishkin et al., 2014: p. 60; Jiang et al., 2017), they were not found in Eastern Europe until the Vyaznikovian time. That is, they were either absent here or belonged to rare marginal elements of the biota, not fixed in the geological record. The noted episode of the bystrowianid expansion at the Permian–Triassic boundary in Eastern Europe, apparently, had a wide spatial expression in the territory of Eurasia (see below). As in the case of the first emerging groups belonging to the number of future dominants, the appearance of bystrowianids in the Vyaznikovian fauna preceded the beginning of their Mesozoic history (limited to the early and middle Triassic of Europe).

The next feature of the Vyaznikovian fauna, which is indicative of its transience and relative instability, is associated with the manifestation of the “Lazarus” effect, i.e., with a short-term “revival” in it of individual groups that seemed to have become extinct much earlier. This includes the unexpected presence here of relicts of the Permo-Carboniferous equatorial biota—Microsauria among amphibians and lungfish of the genus *Gnathorhiza*⁶ (Shishkin and Ochev, 1993; Minikh et al., 2011; Shishkin et al., 2018). Unlike the groups new to the Paleozoic (such as archosaurs), whose appearance in the Vyaznikovian fauna anticipated their flourishing in the Mesozoic, these relicts either disappear already in the Permian or, like the *Gnathorhiza*, do not survive the early Triassic.

Phenomena of similar sort as those noted right above include also the episode of the “return” to the geological record of the narrow-scute member of the family Chroniosuchidae (in the order Chroniosuchia). It is assumed that the Vyaznikovian chroniosuchid *Uralerpeton* is closely related to its only known morphological predecessor, *Suchonica* (Golubev, 1999),

⁶ In the southeast of the East European Platform and in the Southern Cis-Urals, this genus apparently appeared in the Vyatka Stage somewhat earlier (Tverdokhlebov et al., 2005).

which existed in the first half of the Severodvinian time, before the appearance of the Sokolki faunal assemblage. This relationship seems highly probable (Shishkin et al., 2014, p. 65). However, in the case of *Uralerpeton* we do not bear in mind the return of the former dominant group. In fact, both episodes of the existence of narrow-scutate chroniosuchids known to us were equally ephemeral, being equally timed to major biotic turnovers (the second one, to the Late Permian crisis; and the earlier, to the transition from the Middle Permian dinocephalian biota to the faunas of the Sokolki assemblage (Bulanov and Golubev, 2011; Golubev, Bulanov, 2018)). In other words, in both cases these forms were typical “disaster taxa” characteristic of the epochs of biotic re-arrangements. The high variability of dermal scutes in *Suchonica* (Golubev and Bulanov, 2018), with characteristic deviations towards the bystrowianid organization (Shishkin et al., 2014), was apparently also present in the less well-known Vyaznikovian *Uralerpeton*. This feature can serve as an additional indirect indication of the relative instability of the corresponding transitional biotas.

In addition to all the above-mentioned features of the Vyaznikovian fauna, the only known local genus of temnospondyl amphibians, the trimerorhachoid *Dvinosaurus*, exhibits various deviations from the organization typical of the Paleozoic forms. The morphology of its representatives demonstrates here a characteristic picture of increased variability of the phylum on the eve of its extinction, i.e., its “terminal instability” (Shishkin, 2015). The two *Dvinosaurus* species encountered here show drastic mosaic differences, both from each other and from their conservative predecessor *D. primus*, which existed throughout the history of the faunas of the Sokolki assemblage. Most of these differences are at the same time distinct deviations towards the Mesozoic plan of temnospondyl organization. In one case (the species *D. egregius*), this is the development of the posterior vomer processes and the embedding of the carotid arteries into the parasphenoid; in another case (in *D. purlensis*), this is the development of the retroarticular process of the lower jaw and the acquisition of transsegmental integration of the vertebral hemicentra. The alternative-ness of these transformations in the two species gives impression of their divergent evolution; however, in fact, they show the same direction of changes towards the Mesozoic morphotype, manifested in the form of different initial steps (Shishkin, 2019a). Probably, these two Vyaznikovian species of *Dvinosaurus* known to us represent only a part of the spectrum of unstable structural variants that simultaneously emerged on the basis of the original organization of the genus in search of a new model of equilibrium in critically changed conditions. This burst of variability within the genus, with individual grotesque deviations from its original conserved organization, clearly indicates its historically recent emergence.

The very presence of two sharply different and spatially separated *Dvinosaurus* species in the Vyaznikovian fauna (in the basins of the Klyazma and Vyatka rivers, respectively) suggests its local heterogeneity even within the limited territory in which it is known today. The degree of this heterogeneity remains unclear due to the limited availability of material; however, as shown above for the early Triassic faunas, it is a typical feature of transitional non-equilibrium biotas.

With all the changes towards the Mesozoic appearance observed in the terminal Permian tetrapod fauna of Eastern Europe, it remains sharply different from the pioneer early Triassic (Induan) communities that replaced it, not showing any closer similarity with them than at the level of single common families, such as Bystrowianidae or Proterosuchidae. Indirect estimation of the time of separation of the lineages to which the dominants of the local Induan faunas belong (proceeding from the time of the appearance of their closest relatives in the Paleozoic communities) shows that, in most cases, the history of the former began no closer than in the early or middle Permian. In particular, this concerns the two main pioneer families of the Triassic temnospondyl amphibians of Eastern Europe. In this case, both the primitive ancestors of Tupilakosauridae and the only Paleozoic group (Rhinesuchidae) that can be considered closely related to the Capitosauridae appeared in the early Permian (Milner and Sequeira, 2004; Cisneros et al., 2015)⁷. Apparently, even in the case of single families inherited from the Vyaznikovian biota, their earliest early Triassic representatives are not direct descendants of the identified Permian taxa (in particular, this concerns the bystrowianids; see Shishkin et al., 2014). In general, it is obvious that the pioneer Triassic tetrapod fauna of the region arose not as a product of transformation of the terminal Permian assemblage but was formed de novo due to marginal taxa that had more or less long ghost lineages throughout the Permian. In other words, the *systemic transformation of the tetrapod fauna* as a whole during the transition to the Mesozoic looked at the level of its elementary components as a *space of a multitude of disordered historical substitutions*, obviously, at first very unstable and changing over time.

PROBABLE TRACES OF THE “VYAZNIKOVIAN EPISODE” IN EURASIA OUTSIDE EASTERN EUROPE

The possibility of detecting critical terminal changes in regional Permian biotas, similar to those noted for the Vyaznikovian fauna, would suggest, first, a sufficient completeness of collected remains that are

⁷ The concept of a close relationship between Tupilakosauridae and Permian Dvinosauridae, adopted in cladistic schemes (e.g., Yates and Warren, 2000; Schoch and Voigt, 2019), implies a number of misinterpretations of the synapomorphies of these groups (Shishkin, 2011, 2020).

potentially associated with such an event. Second, for a given region, it is necessary that the geological record contains traces of at least two successive faunal episodes, a comparison of which would indicate the mentioned changes. On the territory of Eurasia outside Eastern Europe, among the bone-bearing strata of the late Permian, we do not know sections that adequately meet these two requirements. Nevertheless, based on some specific elements of the Vyaznikovian biota, it can be assumed that the discovery of their analogues in other sedimentary basins may with a high probability indicate the terminal Permian age of the tetrapod communities characterizing them and, indirectly, the unstable state of the latter.

First of all, we bear in mind the bystrowianid chroniosuchians as a family known exclusively in Eurasia. The presence of bystrowianids in three successive intervals of the Middle–Upper Permian of China (Shishkin et al., 2014; Liu et al., 2014; Jiang et al., 2017; Liu and Abdala, 2017), with their late appearance in Eastern Europe, allows the central part of Asia to be considered as the place of the initial radiation of this group, from where it spread both westward and, apparently, eastward (cf.: Arbez et al., 2018; Witzmann et al., 2019). Proceeding from this standpoint, any Central European record of Permian *bystrowianids* cannot be older than the Vyaznikovian *Bystrowiana*. In total, three similar records correlated in age with the named Eastern European genus can be indicated for Eurasia.

Central Europe (Germany)

In the fauna from fissures in the lower Copper Shales (lower Zechstein) near Korbach (Hessen), the bystrowianid *Hassiacoscutum* was described from a single trunk scute (Witzmann et al., 2019); it is undoubtedly close, if not identical, to *Bystrowiana*. Previously, fragmentary remains of therapsids (Late Permian cynodont *Procynosuchus* and indeterminate dicynodont), archosauromorph diapsids (including a form close to *Protosaurus*), as well as small pareiasaurs and a captorhinid with multi-rowed teeth, were identified here (Sues and Munk, 1996). The cited authors, who studied this fauna, attributed it to the early Zechstein, i.e., to the lower (Wuchiapingian) stage of the upper Permian, assuming that the sedimentary fillings containing it are only slightly younger than the host bedrock shales. We do not see sufficient grounds for such a conclusion, taking into account both the very discovery of bystrowianids here and the fact that individual fillings in the local Copper shales actually have different geological ages (some of them contain the remains of Pleistocene mammals (Sues and Munk, 1996)). It seems more likely that the remains of interest belong to the terminal Permian and, thus, to the Changhsingian Stage. This is not contradicted by the presence among them of the cynodont *Procynosuchus*, one of the leading taxa of the ter-

restrial Permian *Daptocephalus* Zone in the Karoo Basin of South Africa (Viglietti et al., 2016), as well as a representative of the captorhinid *moradisaurines*, a group belonging to the dominants of the upper Permian fauna of North Africa (Jalil and Dutuit, 1996; Modesto et al., 2018). We believe that the discussed fauna may be of approximately the same age as the Vyaznikovian community.

China

As already mentioned, bystrowianids are known from the Permian of China from three horizons of different ages. The genus *Yumenerpeton* (Jiang et al., 2017), probably synonymous with the genus *Ingenitidens* (cf. Shishkin et al., 2014) from the same association, described as a chroniosuchid (Li and Cheng, 1999), was found in the Middle Permian dinocephalian fauna of Dashankou in the Gansu province. In the Late Permian Jiyuan fauna from the Shangshihezi Formation in Henan Province, species of three nominal genera were described: *Bystrowiana*, *Jiyuanitectum*, and *Dromotectum* (Young, 1979; Liu et al., 2014). The accompanying tetrapod assemblage (pareiasaurs, gorgonopsians, and cynodonts) indicates an approximate age correspondence to the *Cistecephalus* Zone of South Africa and the Sokolki assemblage of Eastern Europe. Finally, the actual subject of our attention is a bystrowianid not identified to a lower taxonomic level, which was described together with the therocephalian remains from the Goudiken Formation in the Dalongkou section of Xinjiang Province (Liu and Abdala, 2017). The affiliation of the Goudiken Formation to the terminal Permian is determined by the composition of its dicynodonts, in which the “precocious” appearance of the genus *Lystrosaurus* (typical of the Early Triassic) is combined with the presence of *Jimusaria*, a Permian taxon close to *Dicynodon* (Cheng, 1980; Fröbisch, 2009).

Indochina (Laos)

From the Permian–Triassic boundary sediments of the Luang Prabang Basin in Laos, a skull of an unusual chroniosuchian *Laosuchus* with lost otic notches was described (Arbez et al., 2018). The absence of preorbital windows on the skull excludes its assignment to chroniosuchids. Clearly, it belongs either to a specialized bystrowianid, or (which is less likely) to a representative of the common ancestors of the two aforementioned families of chroniosuchians. Among the datings obtained for the bone-bearing tuffaceous sediments of the Luang Prabang Basin (according to zircon analysis data), the most recent ones give the maximum ages of 252.0 ± 2.6 Ma and 251.0 ± 1.4 Ma, i.e., cover the boundary of the Permian and Triassic. The first of them was obtained from the locality where two dicynodonts were found, one of which evolutionarily corresponds to the *Dicynodon* level (i.e., the type of

organization dominating in the Late Permian), and the second is attributed to the kannemeyeriiforms (Olivier et al., 2019). Taken together, this does not clarify the real age of the records, given the fact that the oldest known kannemeyeriiform originate from the basal Triassic of China. The studies of the tetrapod fauna of interest cited above a priori assume that its maximum age is at most 251.0 ± 1.4 Ma. This assumption is based mainly on the traces of zircon grain washing in the host sediments (Olivier et al., 2019). However, the stratigraphic position of the fauna either is not specified (Arbez et al., 2018) or is assumed to be most likely the Triassic, although the possibility of the Permian age is not ruled out as well.

Thus, the probability of a late Permian age for *Lao-suchus* remains fairly high (cf. Bernardi et al., 2017). In this case, the Indo-Chinese record may serve as additional evidence that, at the end of the Permian on the territory of Eurasia, there was a short episode of large-scale latitudinal expansion of the bystrowianids (which was also reflected in the Vyaznikovian fauna).

ACTUAL OR POSSIBLE MANIFESTATIONS OF A NON-EQUILIBRIUM (TRANSITIONAL) STATE IN TERMINAL PERMIAN TETRAPOD COMMUNITIES OUTSIDE EURASIA

South Gondwana

South Africa. The geological record of the Karoo Basin of South Africa is considered one of the main sources of information about the evolution of communities of Permian terrestrial vertebrates. Nevertheless, data on the initial changes in the world of tetrapods associated with the decay of the Permian biota are very scarce in this case. They concern the final Permian fauna of the basin, which characterizes the *Daptocephalus* Zone. The recent clarification of the range of this zone, associated with the revision of the list of its leading taxa (which are now recognized as the dicynodont *Daptocephalus leoniceps* and therocephalian *Therionathus microps*), also led to its division into two subzones (Viglietti et al., 2016). The upper of these corresponds to the well-known appearance here of dicynodont *Lystrosaurus* (the future typical component of the pioneer Triassic biota). This change is, apparently, the only evidence known for the region, indicating the beginning of the rearrangement of the terminal Permian community towards the Mesozoic plan of organization.

An assessment of the taxonomic diversity of the two parts of the *Daptocephalus* Zone, based on several hundred reliably associated bone records, led to the conclusion that it most likely changed little with time, despite the noticeably smaller number of remains in the upper subzone. Accordingly, the assumption that the real mass-scale extinction of the last Permian fauna took place here only in the short final episode of the existence of its upper subzone, is accepted as the

most probable (Viglietti et al., 2016). Objectively, this conclusion agrees little with the previous concept of a “stepwise” extinction of the *Daptocephalus* fauna, based on the presumed presence of traces of several phases of this process in local sediments (Smith and Botha-Brink, 2014). At the same time, the data on the levels of the last occurrence of certain analyzed taxa in sediments, which underlie this concept, often significantly differ from similar subsequent estimates, which may be partly due to differences in the thickness of the compared local sections (Viglietti et al., 2016). However, even if the phenomenon of “stepwise” extinction is to some extent real, in this case it concerns only the stages of depletion of the *Daptocephalus* fauna, but not the appearance of new elements in it—such as predecessors of future dominants or, conversely, “revived” relics of previous biotas. Thus, the majority of the actual manifestations of the transitional (non-equilibrium) state of the South African terminal late Permian fauna still remain hidden from us.

East Africa. Late Permian tetrapod faunas of the South African type with complete predominance of therapsids are also known in the east of the continent, primarily in Malawi (Chiveta Formation), Zambia (Luangwa Basin, Upper Madumabis Formation), and Tanzania (Ruhuhu Basin, Usili Formation). Among them, when compared with the reference communities of the Karoo Basin, the fauna of Usili stands out especially due to the high degree of endemism, as well as due to the joint presence in it of many genera that in South Africa correspond to different age (zonal) intervals (Sidor et al., 2010; Angielczyk et al., 2014a, 2014b).

Against the background of these features of the Tanzanian fauna, the presence of the unique temnospondyl amphibian *Peltobatrachus* among its endemics deserves special attention (within the framework of our study). In modern cladistic attempts in the construction of the Temnospondyli system (e.g., Yates and Warren, 2000; Schoch, 2013), this genus is regarded as a representative of the basal “stereospondyls,” not closely related to any of the Mesozoic groups. However, due to the unusual features of the axial skeleton, this form is close to the Triassic plagiosaurs and, on this basis, can reasonably be considered their early primitive predecessor (Panchen, 1959; Shishkin, 1987; Milner, 1990).

The appearance of this aberrant taxon under the conditions of the nearly complete absence of other temnospondyls (except for the dominant family Rhinesuchidae) in the late Permian of southern Gondwana allows us to make two assumptions with caution. First, it is possible that here we are dealing with an initial disruption of the normal organization of the local biota, which allowed a new component (belonging to the roots of one of the early Mesozoic groups, i.e. plagiosaurs), to gain a foothold in its composition. Second, it is logical to assume that these

events might have taken place just before the end of the Permian, together with other (unknown to us) manifestations of the initial destabilization of the tetrapod community.

It is difficult to verify the reliability of these assumptions today. The Usili fauna is usually compared with the South African *Cistecephalus* Zone (Wuchiapingian Stage), relying not so much on their direct correspondence but on the correlation with this zone of the tetrapod assemblage from the upper Madumabis Formation in Zambia. The synchronicity of this assemblage with the Usili community, in turn, is substantiated mainly by the presence of a common dicynodont species “*Dicynodon*” *huenei* in them (Angielczyk et al., 2014a, 2014b). However, the validity of attributing the Zambian records to this taxon (revised later as the species *Daptocephalus*) is questioned (Kammerer, 2019). In addition, the presence in the Usili fauna of the therocephalian *Theriognathus microps*, one of the guide species of the terminal Permian *Daptocephalus* Zone in South Africa, as well as the record in the Tanzanian fauna of a biarmosuchian (Burnetiidae) resembling the species from the mentioned zone (Sidor et al., 2010), is worth noting. However, the possibility of revising the dating of the Usili fauna towards a younger age per se does not indicate its correspondence to the terminal interval of the *Daptocephalus* Zone. Thus, it remains unclear whether the appearance of the plagiosauroid *Peltobatrachus* actually corresponds to the beginning of crisis changes in the late Permian biota.

Australia and Tasmania. Among the few tetrapods from the eastern part of South Gondwana that are (reliably or presumably) of the Permian age, the brachyopid temnospondyl *Bothriceps* from deposits of the upper Permian Group in the southeast of Tasmania Island deserves special attention (Warren et al., 2011). The lower part of this unit, containing the remains of *Bothriceps*, is generally dated as the transition of the Permian to the Triassic. Sandstones with the remains of an unidentifiable dicynodont (Rozeffelds et al., 2011), directly underlying the *Bothriceps* burial, have an absolute dating of 253 ± 4 Ma, indicating the late Permian as the earliest possible age for them. It should be noted that, in general, brachyopids are known as a Mesozoic group.

Against the background of its typical brachyopid features, the genus *Bothriceps* also shows a mosaic of plesiomorphies that are unusual for the family (such as the shape of the posterior temporal openings of the skull, the presence of foramen chordae tympani in the lower jaw, etc.) and, on the other hand, the transformation of vertebrae into a diplospondylous structure as in Tupilakosauridae (a kind of specialization which is rare among Temnospondyli). This combination of features resembles an example of “archaic diversity,” i.e., evidently indicates that the taxon belongs to one of the basal lineages associated with the early stage of

the formation of the brachyopid organization. This status of *Bothriceps* is consistent with its aforementioned “transitional” dating, with its terminal Permian age being rather probable.

Another example of the “precocious” appearance of the Mesozoic group in the region is the presence of the rhytidosteid temnospondyl *Trucheosaurus* in the upper Permian of New South Wales, Australia (Marsicano and Warren, 1998). However, the interval from which this record was described (the Glen Davis Formation of the Illawarra coal-bearing strata) is dated based on palynomorphs as the Dzhulfian (Wuchiapingian), and thus does not belong to the terminal Permian. If this dating is correct, then the appearance of an early rhytidosteid at the indicated level can hardly be associated with the beginning of the decay of the Permian biota.

North Africa (Central Pangea)

Among the tetrapod communities attributed to the late Permian, the endemic faunas of North Africa, found in the Moradi Formation of Nigeria and the Ikakern Formation of the Argana Basin in Morocco, stand out sharply. They are known from skeletal and trace remains and are associated with equatorial paleolatitudes (Bernardi et al., 2017). The uniqueness of their group composition, as if uniting different-age epochs, allows the assumption that some transitional (relatively short-term) state in the evolution of the regional biota (apparently, on the eve of the late Permian crisis) was recorded in them. In fact, they show a combination of Pennsylvanian–Early Permian in appearance elements with later Permian forms. In the fauna of Nigeria, the former are represented by temnospondyl amphibians of the edopoid evolutionary level, including the proper edopoid (cochleosaurid) *Nigerpeton* and the closely related taxon *Saharostega* (Sidor et al., 2005; Damiani et al., 2006; Steyer et al., 2006; Sidor, 2013). In Morocco, where temnospondyls are poorly known (Steyer and Jalil, 2009), amphibians are dominated by a lespodylid diplocaulid closely related to the North American genera *Diplocaulus* and *Diploceraspis* (Germain, 2010). For the late Permian time, all these elements have the appearance of “living fossils”, inherited from the Euroamerican Permo–Carboniferous biota, which characterized the “Edaphosaurian–Nectridian” equatorial province of Milner (Milner, 1993). The same assessment is partly justified for one of the two main groups of accompanying herbivorous reptiles, captorhinids of the subfamily Moradisaurinae with multi-rowed jaw teeth (Jalil and Dutuit, 1996; O’Keefe et al., 2005; Modesto et al., 2018). Although captorhinids are known to varying degrees throughout the entire Permian (Modesto and Smith, 2001; Reisz et al., 2011), their heyday was also associated with the beginning of this time. The only tetrapod component widely represented in North Africa, which is common for the late Permian in gen-

eral, is pareiasaurs (genera *Bunostegos* in Nigeria and *Arganaceras* in Morocco (Sidor et al., 2003; Jalil and Janvier, 2005; Tsuji et al., 2013; Turner et al., 2015)). Like moradisaurines, in the fauna of Moradi they account for approximately one-third of all records (Bernardi et al., 2017). On the contrary, the skeletal remains of therapsids are either unknown or, in the case of the Moradi fauna, are so far represented by the only fragment presumably attributed to rubidgine gorgonopsians (Smiley et al., 2008).

If the unusual structure of North African communities is hypothetically considered as a transitional unstable state associated with the process of disintegration of the late Permian biota, then it, apparently, should be sufficiently close in time to the final Permian extinction.

However, in reality, the dating of these communities is not completely clear. The presence of diplocaulids in Morocco may suggest their early Permian age (Dutuit, 1988; Milner, 1993; Lucas, 2004). On the other hand, the previous assignment of the considered faunas to the upper Permian (Taquet, 1972) often implied the middle Permian in the current sense. In this case, the dating mainly relied on the comparison of the Moroccan forms (Captorhinidae (Moradisaurinae) and, later, Diplocaulidae) with communities from the Kazanian of Eastern Europe and from its putative equivalent in North America (Taquet, 1972; Jalil and Dutuit, 1996). Finally, the main arguments in favor of the upper Permian dating (prevailing now) is the probable presence of the rubidgine gorgonopsid in the Moradi fauna, as well as the fact that that all the known South African captorhinids belong to this age (Smiley et al., 2008; Tsuji et al., 2013). A more indirect argument is the comparison of the North African ichnofaunas with that of the Val Gardena Formation in the Southern Alps, dated by the upper Permian (Bernardi et al., 2017). The attribution of the discussed African faunas to the specific upper Permian stages, i.e., Wuchiapingian (Sidor et al., 2005, Fig. 2; Hmich et al., 2006) or Changhsingian (Modesto et al., 2018) is indicated rarely and without clear justification.

It should also be noted that the age estimate for the most routine group component of the Moroccan and Nigerian faunas (i.e., pareiasaurs) remains controversial. In both cases, their resemblance to the genus *Elginia* from the Upper Permian of Scotland is noted; however, for the more thoroughly studied Nigerian *Bunostegos*, it is assumed to be convergent, and this taxon itself is placed in an intermediate position between the middle and upper Permian pareiasaurs (Jalil and Janvier, 2005; Tsuji et al., 2013; Turner et al., 2015).

At the same time, the current ideas about the genesis and habitats of the North African Permian faunas are fairly unanimous. The relationship between their archaic elements and the Permo-Carboniferous biota of Euramerica looks self-evident. Only the question of

whether they appeared on the African continent in the early Permian or arrived there later is discussed (Sidor et al., 2005; Steyer et al., 2006; Damiani et al., 2006; Germain, 2010). An increase in aridification during the Permian and, as a consequence, the emergence of an arid belt with a specific biota in the equatorial zone of the Lopingian time is indicated as the main cause for the endemism of local communities. An analysis of the lithology and geochemistry of local bone-bearing strata indicates that the climate was similar to desert, though with pronounced seasons of monsoon precipitation. It is believed that these features, as well as the belonging of North Africa (in the late Permian) to the Euroamerican floristic province, dominated by Voltzian conifers and other gymnosperms, determined the biotic isolation of this region from South Gondwana with its temperate climate and *Glossopteris* flora (Sidor et al., 2005; Steyer et al., 2006; Sidor, 2013; Looy et al., 2016; Bernardi et al., 2017).

The idea of the latitudinal-climatic conditionality of the endemism of the North African faunas was also developed within the framework of a general analysis of the Lopingian continental biotas. According to the hypothesis of Bernardi et al. (2017), the gradient of the latitudinal representation of high-rank tetrapod groups in the Late Permian showed an *increase towards the equator*, which is consistent with a number of previous generalizations explaining in this way the increased diversity of the composition of tropical communities (both extant and extinct). The authors of this hypothesis, as well as many other researchers, associate this feature with the fact that low-latitude environments in general should be characterized by both an *increased rate of emergence of new life forms* and a *slow extinction of old ones*. Thus, it is accepted that both of these patterns (the contribution of which to tropical diversity has been discussed for a long time (Stebbins, 1974)) simultaneously operate at low latitudes. An example of the first effect is the appearance of archosauromorphs (among the future Mesozoic dominants) in the Late Permian communities, and an example of the second is the preservation of archaic amphibians and captorhinids in the North African faunas discussed (Bernardi et al., 2017).

Thus, the two phenomena emphasized above (the “precocious” appearance of evolutionary innovations and the “delayed” disappearance of individual relics) are considered in this case as permanent properties of low-latitude biota; i.e., they receive an exclusively *spatial* explanation. However, according to our notion, as indicated above, both of these phenomena are expected patterns of the systemic re-arrangement of communities and, therefore, have *heterogeneous dynamics over time*. It means that an irreversible disturbance of the biotic system stability under threshold conditions renders it to a *non-equilibrium state*, in which the internal relationships that control its composition weaken and lose their efficiency. As a result, individual marginal components of the community get

an opportunity for a rapid increase in abundance and accelerated stabilization. This equally applies to the *recently emerged variants of life forms and to individual relics of old groups*. This course of events inevitably gives the process of historical transformations of biotas an uneven (intermittent) character, which is not expressed in purely spatial explanations of their causes. This does not dispute the possibility of the leading role of low-latitude environments in the formation of early models of organizational innovations, at least for epochs with sharp latitudinal climate differentiation (the “equatorial pump” effect (Darlington, 1966)). However, the transformation of such models into stable types of organization (the only ones that are fixed by the geological record) hardly has the same unambiguous zonal conditionality.

In light of the above, regarding the causes for the preservation of relics, they can hardly be explained by the “conserving” role of low latitudes. First, associating the formation of new organizational models with the tropics, we thereby recognize the *later consolidation* of the latter at high latitudes, where they can persist longer than in the regions of their emergence (“extraequatorial persistence” (Meyen, 1986)). Second, speaking of fossil relics, we in many cases mean the “return” of a taxon to the available geological record after a certain chronological hiatus. This phenomenon (“Lazarus” effect), reflecting the repeated enhancement of the role of a taxon after a period of its marginalization, obviously indicates systemic changes in the community to which it belongs. However, such changes could occur in different latitudinal zones.

The above-mentioned difference in understanding the causes for the persistence of relics in the composition of advanced communities can be explained using the example of the considered North African late Permian faunas, in which deeply archaic amphibians (edopoid temnospondyls and diplocaulid neotridians) were retained. The spatial (“latitudinal-climatic”) explanation of this fact clearly indicates the source of the origin of these ancient groups, but does not address the issue of the significance of their role in earlier communities that existed closer in time to the Permo-Carboniferous equatorial fauna of Euramerica. On the other hand, within the framework of a systemic view of the mechanism of faunal re-arrangements, the very fact of the anomalous presence of ancient groups in the biota unusual for them makes it possible to assume, with a certain probability, a repeated temporary enhancement of their role following the period of their decay. To confirm this assumption in relation to the North African faunas, data on the previous stages of their evolution during the Permian should be available. Since there is no such information, we can only rely on some indirect evidence.

First of all, they concern the Moroccan diplocaulid (*Diplocaulus minimus*). Of the three known skulls of this taxon, two are preserved sufficiently completely

and show the same type of asymmetry (the shortening and roundness of the right posterolateral angle of the skull). Individual variability is unlikely here, and a possible cause of this aberration is estimated as “environmental stress” (Germain, 2010). However, in our opinion, the interpretation of this phenomenon as an evidence of variability of a phylum on the eve of its extinction is the most probable explanation (cf. Shishkin, 2017, 2019a). We mean that a critical change in the conditions of existence of a “normal” ancestral morphotype made impossible its stable reproduction in generations and led to its replacement by a space of labile variations, one or several of which could stabilize for a short historical time as relatively viable (an example of which is *D. minimus*). In this case, the immediate prehistory of this diplocaulid morphotype, linking it with a normal ancestor, did not represent a number of equally stable forms but showed a decline in abundance and stability of individuals realized during this transition. Then, the morphology of the taxon under discussion apparently indicates its formation on the basis of a non-equilibrium (unstable) organization in the closest ancestors.

Another object of consideration is the prehistory of the moradisaurine captorhinids. Although it is not known specifically for North African genera, it can be roughly estimated for the Permian land in general. The main part of the diversity of moradisaurines, like captorhinids in general, falls on the early Permian of North America. In the middle Permian, there are only represented by rare records from Eurasia related to the dinocephalian fauna (*Gecatogomphius* from the Kazanian Stage of Eastern Europe and *Gansurhinus* from the Sidagou Formation of China (Vyushkov and Chudinov, 1957; Reisz et al., 2011)). In the late Permian, the moradisaurines are again among the regional dominants, in this time in North Africa. In addition, they are known from rare remains in the neighboring regions of Southern and Central Europe (Port de Canonge beds of Mallorca Island and Zechstein of Germany (Sues and Munk, 1996; Liebrecht et al., 2017)). The only coeval record outside these ranges (assigned to the middle Permian species (Reisz et al., 2011)) comes from Inner Mongolia. All other late Permian captorhinids, known entirely from South Africa, are not classified with moradisaurines and belong to small insectivorous forms with largely single-rowed teeth (Gow, 2000; Modesto and Smith, 2001). Thus, the available data on the history of the moradisaurines indicate their extinction in the Guadalupian time with a subsequent local return to the number of dominants by the end of the Permian. Such a picture of the history of this group is similar to the typical “Lazarus” effect, differing only in the weak expression or brevity of the gap in its documented record. It allows us to assume with a high probability that the important role of the moradisaurines for the North African communities was not directly inherited

from the Permo–Carboniferous biota, but developed here de novo.

At the current state of knowledge, it is unclear to what an extent the described processes took place in the course of the formation of North African faunas. Nevertheless, in any case, the very fact of the presence of diplocaulid or edopoid amphibians in the same communities with pareiasaurs clearly indicates that the latter showed features of disequilibrium and developed relatively recently in relation to the time of its recorded existence. This holds true even in the hypothetical case of the North African faunas actually belonging to the middle Permian (see above). In this case, their characteristic manifestations of disequilibrium could correspond to the early stage of the systemic transition from the Guadalupian biota to the Lopingian one.

CONFLICT OF INTEREST

The author declares that he has no conflicts of interest.

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Translated by M. Batrukova