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## ON THE PRINCIPLES OF GLOBAL CORRELATION OF THE CONTINENTAL TRIASSIC ON THE TETRAPODS

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History of the Triassic land vertebrates comprises three successive global epochs referred to as proterosuchian, kannemeyeroide and dinosaur ones. The earliest and the middle epochs are typified by the regional faunal sequence of East Europe. The proterosuchian time spans here the Neorhachitome and *Parotosuchus* faunas, the former being directly correlated with the Induan-Lower Olenekian, and the latter with the Upper Olenekian (Spathian). The *Eryosuchus* and *Mastodonsaurus* faunas of the kannemeyeroide epoch in East Europe are Middle Triassic in age and correspond to the Muschelkalk and Lettenkohle respectively. An evidence is brought for contemporaneity of the proterosuchian-kannemeyeroide biotic replacement in Laurasia and Gondwana. This implies the Middle Triassic age of the *Cynognathus* Zone of South Africa and its equivalents in South America. The bulk of *Lystrosaurus* fauna in Gondwana is suggested to range over the most of, or the whole, Early Triassic.

**Key words:** Triassic tetrapods, biotic epochs, correlation.

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### INTRODUCTION

The Triassic was a time of transition from the late Palaeozoic (therapsid) to the true Mesozoic (archosaur) stage of the tetrapod faunal evolution. This change was one of the most important events in the history of the continental biota and its pattern still remains far from clear. In order to examine it one needs a reliable stratigraphic correlation of the fossil-bearing continental deposits all over the world. On the other hand, it is the tetrapod fauna itself that provides the best means of such correlation. For this reason it has become a subject of the intensive biostratigraphic studies (Romer 1970a; Cox 1973; Anderson and Anderson 1970; Battail 1972; Anderson and Cruickshank 1978; Benton 1983; etc.). Their purpose, however, cannot be restricted to a simple co-ordinating the particular faunas into one or another sort of the correlation charts as it often occurs. The data obtained in such a way should

be analyzed in order to reveal the most universal biotic replacements which could serve as an integral framework for comparing the regional faunal changes.

### EUROPEAN FAUNAL SEQUENCE

Triassic vertebrates are known from all the continents (fig. 1); but their worldwide comparison should be based on those regional sections which contain sufficiently complete and continuous faunal sequences. One of few such opportunities is provided by the Triassic sediments of the Cis-Uralian region (Table 1). The latter is understood here in a broad sense, i.e. as an area extending from the Urals over the whole East European Platform. Extensive geological and palaeontological research which had been carried out in the Soviet Union for two last decades made it possible to improve and complete the biostratigraphic scheme

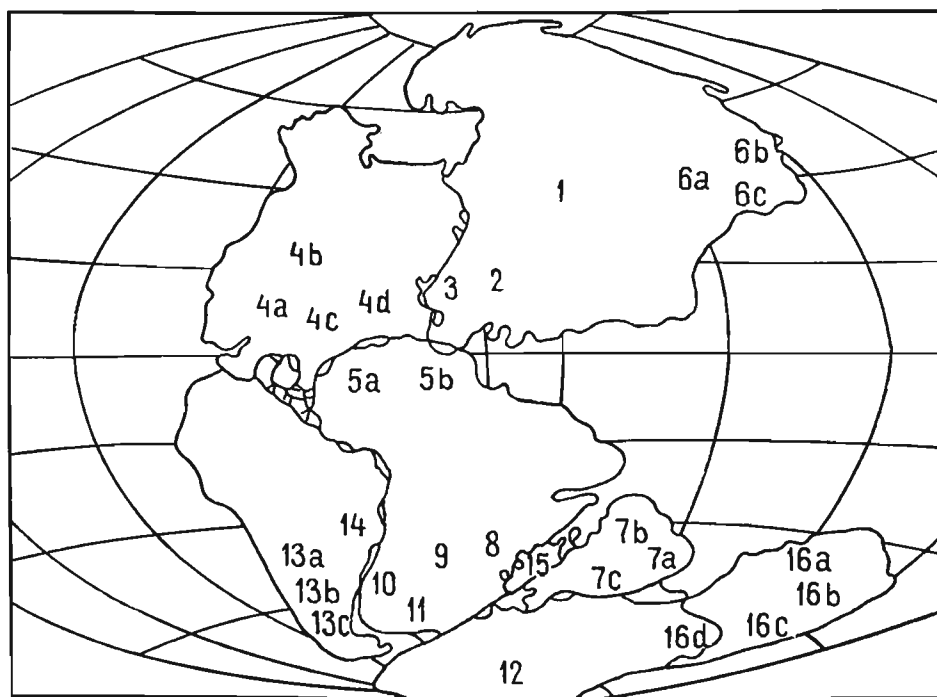


Fig. 1. Principal tetrapod localities in the Triassic continental deposits. 1 Cis-Urals, 2 Central Europe, 3 Britain, 4 North America: a Arizona, b Texas, c Wyoming, d Atlantic Coast, 5 North Africa: a Morocco, b Algeria, 6 China: a Sinkiang, b Shansi, c Yunnan, 7 India: a Northern Coal fields Region, b Central India, c Godavary Valley, 8 Tanzania, 9 Zambia, 10 Namibia, 11 South Africa, 12 Antarctic, 13 Madagascar, 14 Argentina: a Puesto Viejo, b Cacheuta, c Ischigualasto, 15 Brasil, 16 Australia: a West Kimberley District, b Queensland, c New South Wales, d Tasmania.

proposed by Efremov (1937, 1952). This, in turn, permitted to distinguish for the area two major epoches in the tetrapod faunal evolution. The epoches differed in dominant taxa of the superfamilial to ordinal rank (Shishkin and Ochev 1967, 1985; Ochev 1976, 1979; Otshev and Shishkin 1984). The early proterosuchian epoch is marked by the dominance of the primitive thecodonts over other reptiles; the succeeding kannemeyeroïd epoch demonstrates the radiation of anomodonts and the appearance of pseudosuchians (rauisuchids and euparkeriids), the gomphodonts and the advanced bauriamorphs. These two major divisions are also distinguished by their labyrinthodont components. Each of them includes in turn two successive faunas showing a close phylogenetical relationship.

The assemblages of the proterosuchian epoch are of particular biostratigraphic importance for they constitute the only regional sequence so far known among the Triassic tetrapod faunas that permits a direct comparison with the marine sections (due to the presence of common labyrinthodont genera). The earlier (Neorhachitome) fauna of that epoch comes from the Vetlugian superhorizon succeeding to the Tatarian stage of the Permian. It includes three groupings which conform to the respective horizons constituting the Vetlugian unit (Blom *et al.* 1982; Shishkin and Ochev 1985). The lowermost of them, belonging to the Vokhmian horizon, is equated with the Induan of Greenland by the occurrence of the brachyopoid *Tupilakosaurus* and lydekkerinid *Luzocephalus* (Shishkin 1980). The middle grouping, corresponding to the Rybinskian horizon is dominated by the early trematosauroid *Benthosuchus*. Its age is defined on the basis of the presence of the closely related *Benthosphenus* in the Lower Olenekian of the Soviet Far East (Shishkin and Lozovsky 1979). The latest member of the sequence coming from the Sludkian horizon is dominated by the type species of the capitosaurid *Wetlugasaurus* (*W. angustifrons*) and is believed to belong to the upper part of the same substage (Lozovsky 1967).

The succeeding *Parotosuchus* fauna of the proterosuchian epoch is yielded by the Yarenskian horizon which encompasses the upper part of the Lower Triassic in the Cis-Urals. The labyrinthodont components *Parotosuchus* and *Trematosaurus* (the type genera of two respective families), which dominate here, provide a correlation with the Upper Olenekian estuarine and coastal deposits of the Caspian Depression and (*Parotosuchus*) the Mangyshlak Peninsula (Lozovsky and Shishkin 1974). The same forms occur in the Middle Buntsandstein of Central Europe (Hardeggen Beds).

The record of the kannemeyeroïd epoch in the Southern Cis-Urals begins with the *Eryosuchus* fauna. This is produced by the upper part of the Donguz Formation which overlies here the equivalents of the Yarenskian horizon (well documented by the tetrapod evidence). Amongst reptile components of this fauna the kannemeyeroïd anomodonts are most

Table 1  
Distribution of tetrapods in the Triassic of the Cis-Urals

LOWER TRIASSIC		MIDDLE TRIASSIC		Epochs	
Wetlugasaurus-Benthosuchus	Parotosuchus	Eryosuchus	Mastodonsaurus	Faunas and groups	Systematic composition
				<i>Tupilakosaurus</i>	1
				<i>Batrachosuchoides</i>	
				<i>Benthosuchus</i>	
				<i>Thoosuchus</i>	
				<i>Prothosuchus</i>	
				<i>Angusaurus</i>	2
				<i>Trematotege</i>	
				<i>Trematosaurus</i>	
				<i>Inflectosaurus</i>	
				<i>Yarengia</i>	
				<i>Luzoscephalus</i>	
				<i>Wetlugasaurus</i>	
				<i>Parotosuchus</i>	3
				<i>Eryosuchus</i>	
				<i>Bukobaja</i>	
				<i>Mastodonsaurus</i>	
				<i>Melanopelta</i>	
				<i>Plagiosturnum</i>	4
				<i>Plagioscutum</i>	
				<i>Phaanthosaurus</i>	
				<i>Contritosaurus</i>	
				<i>Tichvinakia</i>	
				<i>Burtensia</i>	
				<i>Vitalia</i>	
				<i>Cosiodontognathus</i>	
				<i>Macrophon</i>	
				<i>Kapes</i>	
				<i>Orenburgia</i>	
				<i>Scalopognathus</i>	5
				<i>Stilphedonuchus</i>	6
				<i>Dongusaurus</i>	7
				<i>Rhynchomphodon</i>	8
				<i>Galeosaurid g. n.</i>	9
				<i>Scalenodon</i>	10
				<i>Antecosuchus</i>	
				<i>Lystrosaurus</i>	
				<i>Radiodromus</i>	
				<i>Rhabdosaurus</i>	
				<i>Rhynchocynodon</i>	
				<i>Uralokannemeyeria</i>	11
				<i>Edaxosaurus</i>	
				<i>Colleonasus</i>	
				<i>Elephantosaurus</i>	
				<i>Elatosaurus</i>	
				<i>Chasmatosuchus</i>	
				<i>Exilisuchus</i>	
				<i>Gamosaurus</i>	
				<i>Garjainia</i>	12
				<i>Erythrosuchus ?</i>	
				<i>Chalishevia</i>	
				<i>Vjushkovisaurus</i>	
				<i>Energosuchus</i>	13
				<i>Jushatyria</i>	
				<i>Scharschengia</i>	
				<i>Microcnemus</i>	
				<i>Blomosaurus</i>	
				<i>Boreopriosa</i>	
				<i>Malutinisuchus</i>	
PROTEROSUCHIAN		KANNEMEYEROID		Faunal epochs	
					LAURINIFORMIA
					PROLOPHONTIA
					THERIOPONTIA
					ANOMOPONTIA
					ARCHOSAURIA
					LEPIDOSAURIA

1 Brachyopoidea, 2 Trematosauroida, 3 Capitosauroida, 4 Plagiosauroida, 5 Ictidosuchia, 6 Scalopocynodontia, 7 Bauriamorpha, 8 Procynosuchia, 9 Cynognathia, 10 Lystrosauridae, 11 Kannemeyeroidea, 12 Proterosuchia, 13 Raurisuchidae.

common and diverse and accompanied by the advanced proterosuchians (erythrosuchids), the rauisuchid and euparkeriid pseudosuchians (Ochev 1981, 1982; Sennikov 1989), the traversodontid gomphodonts and the bauriamorphs. The guide amphibian, capitosauroid *Eryosuchus*, occurs together with the plagiosaurids, *Plagiosturnum* and *Plagioscutum*. The latter is represented by an early species comparable and most probably contemporary to the primitive member of *Plagiosuchus* from the Upper Muschelkalk assemblage of Central Europe (Shishkin 1986a, 1986b, 1987). This correlation would seem to be supported by the occurrence of the capitosauroid "*Mastodonsaurus*" *silesiacus*, an apparent *Eryosuchus* representative, in the Muschelkalk (Ochev 1966). The assemblage of the Muschelkalk (probably the late Anisian to early Ladinian in age) is nearly devoid of reptiles being predominantly marine in origin, but one poorly determinable kannemeyeroïd ("?*Placerias*") was still reported from here.

The next phase of the kannemeyeroïd epoch is represented in the Cis-Urals by the *Mastodonsaurus* fauna in which the most common reptiles are the advanced kannemeyeroïds and the rauisuchid pseudosuchians (Ochev 1980, 1982, 1986, Kalandadze and Sennikov 1985, Sennikov 1989). A wide occurrence of the labyrinthodont "*Mastodonsaurus*" *torvus* (closely related to *Mastodonsaurus*) together with the advanced species of *Plagioscutum* comparable to the late form of *Plagiosuchus* clearly justifies correlation of this assemblage with that of the Lettenkohle (Lower Keuper) of Central Europe. The Lettenkohle reptiles are still poorly known. Among them, there have been recently recovered a rauisuchid pseudosuchian, a prolacertilian and probably cynodonts (Wild 1980). The Lettenkohle is usually assigned to the Upper Ladinian (Anderson and Cruickshank 1978; etc.) and, hence the kannemeyeroïd epoch as a whole seems to cover rather fully the range of the Middle Triassic. This conclusion is in accord with the palaeofloristic evidence (Dobruskina 1968).

The analysis of the record of two biotic epoches outlined above reveals the break in the faunal sequence of the Cis-Urals corresponding to the Upper Buntsandstein assemblage of Central Europe. This includes the capitosauroid *Stenotosaurus*, the early mastodonsaurid *Heptasaurus* and the advanced benthosuchid *Eocyclotosaurus*, the latter being reported to occur together with the advanced prolacertilians (Ortlam 1970). Judging from the palaeofloristic evidence, their age is almost certainly Anisian (Shishkin 1980; Lucas and Morales 1985). Such a dating seems to suggest the assignment of this fauna rather to the beginning of the kannemeyeroïd epoch. Its equivalent may be suspected in the Middle Triassic of the Pechora Depression where a form comparable to *Heptasaurus* has been recovered (Shishkin and Ochev 1967).

Younger Triassic faunas have not been found in the Cis-Urals but they are known in Central Europe from the Middle and Upper Keuper.

Epochs		Land tetrapod findings from marine deposits (outside of Central Europe)	Cis-Urals	Central Europe	Britain	North America	North Africa	China
Stage	Triassic							
Upper	Morian			Oberkeuper 13, 14, 22 Knollenmergel Stubensandstein 13, 23, 24, 25 Blassensandstein 13, 14, 21 Schlitsandstein 13, 14	Bristol Channel 36, 36'	L. Newark Group Dockum, Chinle Fms. 14', 22, 23, 25 Dockum (early assemblage), Pope Agie 14', 15', 21, 25		Lufeng Formation and its equivalents
	Carnian							
Middle	Ladinian	27 (Tessinian Alps)	Bukobay Fm. (Mastodonsaurus fauna) 10', 11, 12 Donguz Fm. (Eryosuchus fauna) 9, 10', 11, 20, 29, 33	Lettenkohle 10, 11, 12 Ober 10, 11, 13, 27 Mittler Unter 9? Roth 15, 16, 27	„Keuper“ Sandstone 6' ?			Ermaying Formation
	Anisian							9', 29'
Lower	Upper	5, 8 (Caspian Depression)	Varenskian Horizon (Parotosuchus fauna) 5, 7, 8					
	Lower	4' (Soviet Far East) 17 <sup>11</sup> , 18 (Spitzbergen) 17 <sup>11</sup> , 18 <sup>1</sup> (Madagascar) 17 <sup>11</sup> (N. Siberia)	Studkian Horizon 3, 4 Rybinskian Horizon 4					
Induan		1, 2 (E. Greenland) 17 W. Australia	Vokhmian Horizon 1, 2, 3, 4, 30	Unter				
								19, 30

Table 2 (continued)

India	Tanzania	Zambia	Namibia	South Africa	South America	Australia Tasmania	Vertical range of principal tetrapod groups	Faunal epochs
Maleri, Tiki Formations 14, 21, 28 <sup>11</sup>	Manda Formation 28 <sup>1</sup>			Lower Elliot Fm.  Molleno	Los Colorados Formation  Ischigualasto, Santa Maria (v. member) Fms. 26, 28	Wianamatta Group 13 <sup>1</sup>	Placiosauroidea Metoposauroidae Rhynchosauria Kannemeyroidae Bauriamorpha Cynognathia Pseudosuchia Pseudosuchia (armoured families) Phytosauria Dinosauria	Faunal epochs
Yerrapalli Formation  9 <sup>1</sup> , 32, 34?	9 <sup>1</sup> , 31, 33	Ntawere Fm.  71, 9 <sup>1</sup> , 31, 32, 35	Omingonde Formation  31, 34, 35	Cyno-gnathus Zone  6, 7 <sup>1</sup> , 8 <sup>1</sup> , 20, 31, 34, 35	Chañares Santa Maria (l. member) Formations  Puesto Viejo, Rio Mendoza Formations	Hawkesbury Sandstone  -- ? --	Lystrosauridae Procynosuchia Proterosuchia Caninemeyroidae Bauriamorpha Cynognathia Pseudosuchia Pseudosuchia (armoured families) Phytosauria Dinosauria	Dinosaur
Mangli, Panchet Formations  1, 19, 30				Upper Beaufort Series Lystro-saurus Zone  17 <sup>1</sup> , 19, 30		Kockatea, Blina, Knocklofty, Gosford, Rewan, (Arkadia) Formations  2 <sup>1</sup> , 5?, 17, 18 <sup>11</sup>	Proterosuchian Caninemeyroid Kannemeyroid Dinosaur	Proterosuchian

*Peltostega*, 17<sup>II</sup> *Boreopelta*, 17<sup>III</sup> *Machavisaurus*, 17<sup>IV</sup> *Pneumatostega*, 18 *Aphaneramma*, 18<sup>I</sup> *Wantzosaurus*, 18<sup>II</sup> *Erythrobatrachus*. Thecodontia: 19 *Proterosuchus*, 20 *Erythrosuchus*, 21 *Palaeorhinus*, 22 *Rutiodon*, 23 *Nicrosaurus*, 24 *Myrstriosuchus*, 25 *Angistorhinus*, 26 *Aetosaurus*, 26<sup>I</sup> *Aetosauroides*. Lepidosauria: 27 *Tanystropheus*, 28 *Scaphonyx*, 28<sup>I</sup> *Supradapedon*, 28<sup>II</sup> *Hyperodapedon* (= *Paradapedon*). Anomodontia: 29 *Rhinodictyonodon*, 29<sup>I</sup> *Shansiodon*, 30 *Lystrosaurus*, 31 *Kannemeyeria*, 32 *Rechnisaurus*. Theriodontia: 33 *Scaledodon*, 34 *Trirachodon*, 35 *Diademodon*. Mammalia: 36 *Morganucodon*, 36<sup>I</sup> *Eozostrodon*, 36<sup>II</sup> *Megazostrodon*. Dash-dot lines indicate the levels which may be roughly correlated with the standard marine scale. Dotted lines correspond to the levels used for regional correlations. Rhaetian is considered as a part of Norian.

This part of the section corresponds roughly to the whole Upper Triassic although its more precise calibration against the marine stratigraphic scale based on various evidence is a matter of debate (Benton 1986). The problem is even more complicated by the fact that the validity of the Rhaetian as a member of this scale is increasingly questioned.

The amphibian component of the late Triassic faunas includes plagiosaurs, cyclotosaurs and metoposaurs which seem to range up to the top of the Keuper (for metoposaurs, see Kuhn 1939). The reptilian finds begin with the upper part of the Gypskeuper and belong mainly to phytosaurs, pseudosuchians and dinosaurs. The latter are known to extend down to the Stubensandstein level although some very doubtful remains were reported even from the Lettenkohle (Huene 1932; cf. Benton 1983).

To sum up, the faunas of East and Central Europe together form a rather close and informative sequence which should be further tested as a possible basis for correlating the tetrapod-bearing Triassic formations from all over the world (Table 2).

#### LAURASIAN FAUNAS OUTSIDE THE CONTINENTAL EUROPE

In North America, the earliest known Triassic faunas come from the Moenkopi Formation of Arizona. They are composed mainly of amphibians and, hence, their allocation among the principal biotic epoches could be made only in indirect way. The basal Moenkopi member, Wupatki, comprises in particular, the capitosauroid *Wellesaurus* (Lehman 1971) which looks as an immediate forerunner of *Stenotosaurus* from the Upper Buntsandstein of Europe and, thereby, may be well contemporary to the *Parotosuchus* fauna. This seems to indicate the proterosuchian epoch. The assemblage of the top member, Holbrook, is dominated by *Eocyclotosaurus* which is found also in the Santa Rosa Sandstone of New Mexico (Lucas and Morales 1985) and recorded elsewhere in the Upper Buntsandstein (Ortlam 1970). This strongly evidences the early Anisian age of the assemblage (see above) and suggests relating it to the earliest phase of the kannemeyeroide epoch. Such a dating seems to be in accord with the occurrence of the poorly known rauisuchid (?) pseudosuchian *Arizonasaurus* in the Holbrook. Anyway, the idea of the time gap between the Upper Buntsandstein and Holbrook faunas, the former being assigned to the Spathian and the latter to the early Ladinian (Anderson and Cruickshank 1978, Benton 1983), cannot be justified.

Younger Triassic faunas come principally from the Chinle Formation of Arizona, the Dockum Formation of Texas and New Mexico, the Popo Agie Member of the Chugwater Formation in Wyoming and the basal members of the Newark Group on the Atlantic coast. As is well known, these faunas are much similar (especially at the familial level)



to those from the Middle to Upper Keuper, being dominated by the metoposaurid labyrinthodonts (*Eupelor*) phytosaurs and pseudosuchians associated with dinosaurs. A more detailed correlation seems possible on the basis of phytosaur genera. The presence of *Palaeorhinus* (*Parasuchus*) in the Popo Agie and the early Dockum faunas suggests the same age as that of the Blasensandstein level of the Keuper whereas the younger age of other listed assemblages is evidenced by occurrence of *Nicrosaurus* which is known elsewhere from the Stubensandstein (Gregory 1969; Chatterjee 1986).

In Britain, the earliest known Triassic assemblage comes from the "Lower Keuper" Sandstone. Of a number of capitosauroid labyrinthodonts recorded here (Paton 1974) "*Cyclotosaurus*" *leptognathus* is the best known and looks extremely similar to *Stenotosaurus* from the Upper Buntsandstein (Shishkin 1980). This would imply the Anisian age of the fauna. On the other hand, its reptilian component is believed by Walker (1969) to indicate the Lower to Middle Ladinian. Both these datings suggest the middle biotic epoch. The fauna from the Lossiemouth Formation of Elgin, Scotland, dominated by pseudosuchians and containing a solitary dinosaur (*Saltopus*), is clearly of the Late Triassic age. The most important correlative is the rhynchosaur *Hyperodapedon* whose supposed congener (described as *Paradapedon*) is known from the Maleri Formation of India (Benton and Walker 1985). The lack of phytosaurs is peculiar and unusual of the late Triassic faunas of the northern continents. One more Triassic fauna pertaining to the dinosaur epoch is known from the oldest group of the fissure fillings of Bristol area. The dinosaurs are associated here with the gliding lepidosaur *Kuhneosaurus*, a member of family known also from Lockatong Beds of the Newark Group in North America. Both the latter unit and the Lossiemouth Formation are tentatively assigned to the late Carnian (Benton 1986).

In the Soviet Asia, the only collecting area from which the late Triassic tetrapods are known is the Madygen locality in the southern part of the Fergana Depression (Tadjikistan). It yielded the gliding reptiles (Sharov 1970, 1971) and the advanced theriodont standing close to the mammalian level (Tatarinov 1974, 1980).

The sequence of principal biotic epoches revealed in Europe can be traced in China (Young 1964, 1966, 1973; Sigogneau-Russell and Sun 1981; etc.). The reptiles are predominant through all the faunas recorded from here. The proterosuchian epoch is represented by the tetrapod complex from the Jimusar Beds (Sinkiang) whose principal components, the anomodont *Lystrosaurus* and the proterosuchian *Proterosuchus* (*Chasmathosuchus*) are typical of the early Triassic of Gondwana. The former has been also found at the base of the Vetlugian superhorizon of the Cis-Urals (Kalandadze 1974, Lozovsky 1983).

The kannemeyeroïd epoch is documented by the *Sinokannemeyeria*

complex produced by the Ermaying Series of Shansi and Sinkiang. It is composed mostly of the same reptilian groups that constitute the Middle Triassic faunas in the Cis-Urals although, at present state of knowledge, no common genera can be detected in these faunas with certainty. The shared groups include the shansiodontid kannemeyeroïds, gomphodonts (though represented by the distinct families, cf. Battail 1977), erythrosuchids and pseudosuchians (rauisuchids and euparkeriids). The idea of the occurrence in the Ermaying assemblage of the proterosuchian *Garjainia* (*Vjushkovia*) peculiar to the *Parotosuchus* fauna of East Europe (Young 1973) is misleading (Kalandadze and Sennikov 1985). Similarly, the only labyrinthodont of the discussed complex, described as *Parotosuchus* (*Parotosaurus*) *turfanensis* (Young 1966) actually belongs to a more advanced genus and is comparable with the Middle Triassic forms in the structure of its vertebrae. The anomodont *Shansiodon* closely resembles the shansiodontid *Rhinodicynodon* from the *Eryosuchus* fauna albeit looks somewhat less specialized (Kalandadze 1970). All these facts provide strong evidence for assigning the Ermaying assemblage to the Middle Triassic rather than the Spathian, in contrast to the predominant belief (Ochev and Shishkin 1988; Battail 1983; Zhen *et al.* 1985).

The younger fauna comes from the Lower Lufeng Formation of Yunnan and is composed mainly of dinosaurs, tritylodonts and primitive mammals associated with pseudosuchians, crocodyles and some other groups. Its stratigraphic position is a matter of debate. Most of recent investigators assign it to the "Rhaeto-Liassic" or the Lower Jurassic only (Olsen and Galton 1977, 1984; Benton 1983; cf. Sun *et al.* 1985). The problem is further complicated by the presence of most archaic components of the fauna, i.e. the labyrinthodonts and phytosaurs, just in its upper grouping. The remains of the late labyrinthodonts are reported also from Shansi, but their assignment to metoposaurids (Huene 1958) seems arbitrary.

#### GONDWANA FAUNAS

In North Africa, the oldest Triassic tetrapod assemblage so far recovered is produced by the Lower Sandstone of the Zarzâitine Series in Algeria. It is known very imperfectly and composed mostly of amphibians whose evolutionary level suggests the Spathian to Anisian age. The scarce fossils from the upper part of the Lower Sandstone seem to indicate the dinosaur epoch (Lehman 1971). A much more abundant fauna of similar age has been yielded by the middle member of the Argana Series in Morocco (Dutuit 1972, 1976, 1977, 1978a, 1978b, 1980 etc.). The metoposaur amphibians and phytosaurs are most common here and found together with the dinosaurs, the advanced kannemeyeroïds

and the rauisuchid (?) pseudosuchians. The phytosaur genera *Palaeorhinus* and *Angustorhinus* (either the former or both) are correlatives with the basal faunal groupings of the late Triassic of North America (Popo Agie, Lower Dockum) and Central Europe (Blasensandstein).

The data on the Triassic tetrapods from India (Chowdhury 1965, 1970; Robinson 1967; Tripathi 1969, 1975; Chatterjee 1986, 1987; Chatterjee *et al.* 1969; Chatterjee and Hotton 1986) provide further evidence for the relevance of the triple biotic division suggested above. The *Lystrosaurus* fauna from the Upper Panchet Series (Hirapur Beds) corresponds to the proterosuchian epoch. Apart from its typical components, *Lystrosaurus* and *Proterosuchus*, it includes a variety of poorly known amphibians showing mainly the lydekkerinid and trematosauroid affinities. Most remarkable is the occurrence of the aberrant brachyopoid *Tupilakosaurus* which provides a direct correlation with the lowermost (Induan) grouping of the Cis-Uralian Neorhachitome fauna (Shishkin 1961, 1980, Lozovsky 1969). The record of the succeeding epoch is provided by the Yerapalli fauna which is close to the *Eryosuchus* fauna from Europe and its equivalent from China. Of its principal elements, the kannemeyerooids are most common and associated with erythrosuchid, rhynchosaur, the poorly recorded gomphodont, and the advanced capitosauroid described as *Parotosaurus* but being in fact a close relative of *Eryosuchus*. Finally, the dinosaur epoch is represented in India most fully by the fauna from the Maleri Formation which includes the theropod dinosaur (*Walkeria*) and shows a close affinity with the Lower Dockum fauna of North America. The reptilian genera shared by both are the stagonolepidid pseudosuchian *Typothorax*, protosauroid *Malerisaurus* and phytosaur *Palaeorhinus* (*Parasuchus*). The latter form as well as the amphibian *Metoposaurus* are also correlatives with the assemblages of the basal Middle Keuper in Europe and the Argana in North Africa. The dominance of the rhynchosaur *Hyperodapedon* (*Paradapedon*) provides a correlation with the Lossiemouth fauna of Scotland.

One of the most important sources of data on the history of the Triassic tetrapods is the faunal succession from the Upper Beaufort Series of South Africa. Its earlier member, the assemblage of the *Lystrosaurus* Zone (paralleled by that of the early Triassic Fremouw Formation of Antarctic; see Colbert 1975, 1977b, Colbert and Kitching 1977, Kitching *et al.* 1972, etc.) is succeeded by the assemblage of the *Cynognathus* Zone (= *Kannemeyeria* Zone of Keyser and Smith 1978). Both faunas are dominated by therapsids. Taken together, they are considered almost unanimously as a standard sequence which should be used for correlation of any early Triassic fauna from around the world (Romer 1970a, etc.). However, in evaluating these faunas in terms of the principal biotic replacements discussed above we encounter the obvious problem with their dating that did not attract too much attention so far. It concerns two

points: the age of the *Cynognathus* fauna and the time range of the antedating assemblage.

The *Cynognathus* fauna displays most of groups which are peculiar to the kannemeyeroïd epoch in the areas concerned above, including kannemeyeriids, gomphodonts, the advanced bauriamorphs and the euparkeriïd pseudosuchians. In this respect it roughly conforms, for example, to the *Eryosuchus* fauna of Europe (differing most considerably in the abundance of therapsids at the expense of amphibians) but looks unlike the antedating *Parotosuchus* fauna. Further on, the changes observable on passing from the *Lystrosaurus* to *Cynognathus* fauna much resemble those on the transition from the *Parotosuchus* to *Eryosuchus* fauna. Of thirteen tetrapod groups common to both earlier faunas, ten had the similar fate at the boundaries compared (Ochev 1983). All these facts would seem to indicate rather clearly that the *Cynognathus* fauna is younger than *Parotosuchus* one (dated as the Spathian) and thereby should be placed in the Anisian. The only conceivable alternative is to admit that the kannemeyeroïd biota had spread over the Southern Gondwana as early as the late Scythian when the typical faunas of the preceding epoch still had populated the northern areas.

Although the latter solution would be possible it does not yet appear much convincing. The assignment of the *Cynognathus* Zone to the Scythian was primarily based on the evidence from its amphibians which were believed to correspond to those from the "*Capitosaurus*" Zone of Europe dominated by *Parotosuchus* and *Trematosaurus* (Efremov 1937, Watson 1942). But this view can hardly be supported at present. The South African forms assigned to *Parotosuchus* seem to be more advanced than their alleged congeners from Europe (Ochev 1966). One more amphibian of the *Cynognathus* fauna long considered as a Scythian element, the brachyopid *Batrachosuchus*, has been recently recovered in the Middle Triassic of Zambia (Chernin 1977). On the other hand, its closest relative from the *Parotosuchus* fauna (*Batrachosuchoides*) was more primitive by retaining the lacrimal and the exoccipital-pterygoid fissure (Shishkin 1966). The data on the occurrence of the early Triassic family Rhytidosteidae in the *Cynognathus* Zone has not been confirmed (Cosgriff and Zawiskie 1979). Although the trematosaurid occurrence seems to be well established, the importance of this family as a marker of the Scythian has become weakened due to recent discovery of its member (*Denwasaurus*) in the Middle Triassic of India and the re-assignment of the problematic *Hyperkynodon* from the Keuper of Europe to Trematosauridae (Chatterjee and Hotton 1986; Hellrung 1987). It may also be noted that the stratigraphic position of the most informative trematosaurid find from the Upper Beaufort, the type of *Trematosaurus sobeyi*, is not quite certain (Kitching 1978). An additional piece of evidence for the age of the *Cynognathus* assemblage can be derived from its

proterosuchian component, *Erythrosuchus africanus* which resembles a large erythrosuchid *E. magnus* from the *Eryosuchus* fauna rather than a more primitive *Garjainia* associated with the *Parotosuchus* fauna (Ochev 1981).

At the same time it seems obvious that the *Cynognathus* assemblage could not be equated exactly with the above discussed kannemeyeroïd communities. Among reptiles, the South African forms *Kannemeyeria* and *Euparkeria* are more primitive than the members of the respective families from the Donguz and Ermaying formations (Kalandadze 1970; Sennikov 1989). The same is the case for the small rhynchosaur, *Howesia* and *Mesosuchus* as compared with their advanced relatives from the Yerapalli Formation of India and the contemporary Manda Formation of Tanzania (Benton 1983). These facts suggest that the *Cynognathus* fauna represents early phase of the kannemeyeroïd epoch but they do not disprove the evidence for its post-Scythian age.

In this connection we must consider a problem of range of the *Lystrosaurus* Zone which has been long dated in the lower half or, more recently (Anderson and Cruickshank 1978), at the very base of the Scythian and considered roughly as an equivalent of the Neorhachitome Zone of Europe. Coupled with the above re-dating of the *Cynognathus* Zone, this would then imply a chronological gap between both South African faunal assemblages corresponding to the range of the *Parotosuchus* fauna in Europe. Such a conclusion seems to be in agreement with a rather sharp difference in composition between two assemblages discussed, which is sometimes believed to indicate the break in the Upper Beaufort faunal succession (Cosgriff 1984). Alternatively, it may be assumed that the *Lystrosaurus* fauna had ranged in South Africa through the whole or the most of Scythian, thus, being correlative of both Neorhachitome and *Parotosuchus* faunas. This idea could be supported by the presence of the capitosauroid (mastodonsaurid) *Kestrosaurus* in the *Lystrosaurus* Zone and by similar evidence from the early Triassic of Australia (see below).

The *Cynognathus* fauna of the Upper Beaufort is most probably paralleled by that from the Omingonde Formation of Namibia. A younger phase of the kannemeyeroïd epoch is recorded in East Africa in the Manda Formation of Tanzania and the Ntawere Formation of Zambia. The elements of the *Cynognathus* fauna like *Kannemeyeria* or (in the case of the Ntawere assemblage) the gomphodont *Diademodon* and the brachyopid *Batrachosuchus* are associated here with the advanced kannemeyeroïds, the traversodontid gomphodonts and the rauisuchid pseudo-suchians. The occurrence of the *Eryosuchus*-looking capitosaurids ("*Parotosaurus*" *pronus*, "*P.*" *megarhinus*; Howie 1970, Chernin and Cosgriff 1975) and the traversodontid *Scalenodon* (in the Manda assemblage) suggests a correlation with the Donguz Formation of Cis-Urals where the

latter genus was detected (solitary tooth, Tatarinov 1974). The kannemeyeroïd *Rechnisaurus* is shared by the Ntawere assemblage and that of Yerapalli from India. For the main Manda assemblage is notable the abundance of the rhynchosaur component (*Stenaulorhynchus*), a condition more common to the later members of the Gondwana faunal successions (Benton 1983).

The tetrapods of the late biotic epoch are known in South Africa from the Lower Stormberg Series (the Lower Elliot Formation) dated tentatively as Carnian or early Norian. They include mostly dinosaurs associated with the rauisuchid pseudosuchians and the traversodontid gomphodont. The labyrinthodont remains are scarce and possibly belong to capitosaurids (Dutuit and Ginsburg 1982, Olsen and Galton 1984). No phytosaurs are found though in the adjacent area (Madagascar, the Upper Isalo Series) they are recorded together with metoposaurus (Guth 1963, Dutuit 1978b).

The next important faunal succession to be considered is that of South America (Bonaparte 1966, 1974, 1982; Romer 1970b; Barberena 1977, 1982; etc.). The principal assemblages of this area known from Argentina are mostly well-coordinated albeit coming from a number of isolated sedimentary basins. They may be rather easily sorted out against the sequence of biotic divisions traced on other continents. Peculiar to most of these assemblages is the extreme rarity or the total absence of the labyrinthodont finds.

The faunas of the proterosuchian epoch are not recorded from Argentina; data on the occurrence of the *Lystrosaurus* fauna reported by Bonaparte (1981) seem rather vague. The earlier assemblage corresponding to the Puesto Viejo Formation equals to the *Cynognathus* fauna of South Africa by the presence of *Cynognathus* and *Kannemeyeria* and is peculiar for the first appearance of the traversodontid gomphodonts. A contemporary assemblage is that of the Rio Mendoza Formation. The later phase of the kannemeyeroïd epoch is documented by the fauna of the Chañares Formation including, in particular, advanced kannemeyeroïds (of which *Dinodontosaurus* is the most common), pseudosuchians (rauisuchids, ornitosuchids and others) and abundant traversodontids dominated by *Massetognathus*. The record of the dinosaur epoch begins with the assemblage of the Ischigualasto Formation assigned most often to the Carnian. In general, it shows the decline of therapsids towards the end of its range while the archosaurs increase in the variety and abundance. These include pseudosuchians (of which the stagonolepidids first come to rise) and a number of dinosaurs. In the succeeding fauna of the Los Colorados Formation the dinosaurs become predominant.

A position of certain other faunas remains open to discussion. In Argentina, it is the case for the assemblage from the Cacheuta Formation which is peculiar in being composed mainly of labyrinthodonts,

*Pelorocephalus* and *Chigutisaurus*. Most of recent authors, following Reig (1961), synonymize these genera and consider *Pelorocephalus* the type genus of the aberrant family Chigutisauridae. Bonaparte (1974) equates the Cacheuta fauna with that of Ischigualasto on the basis of the occurrence of "*Pelorocephalus*" (*Chigutisaurus*) in the latter. Other authors correlate the Cacheuta with the Puesto Viejo. In seeking the proper solution, we must emphasize that, on the evidence provided by the original description (Cabrera 1944), *Pelorocephalus* seems very distinct from *Chigutisaurus* and bears close resemblance to the Middle Triassic brachyopid *Batrachosuchus* from South Africa (Shishkin 1987). This conclusion combined with the presence of the erythrosuchid *Cuyosuchus* implies the allocation of the Cacheuta assemblage in the kannemeyeroide epoch (Puesto Viejo — Chañares time span).

No consensus still exists on the relative position of the Santa Maria assemblage from Brazil (Bonaparte 1982; Benton 1983, 1986) although it seems rather well comparable with the succession recorded from Argentina. This fauna includes in fact two groupings (Barberena 1977, 1982) the earlier of which, composed mainly of therapsids, can surely be equated with the Chañares assemblage due to the presence of *Dinodontosaurus* and *Massetognathus*. Remarkable is the very fact of the anomodont abundance (Benton 1983) common in the kannemeyeroide epoch. The later grouping conforms to the Ischigualasto fauna by the occurrence of dinosaurs and the abundance of the rhynchosaur *Scaphonyx*.

The analysis of the fossil record from Australia is biased by the extreme paucity of the reptilian remains and probably the endemic status of many amphibian genera. The data available so far make an impression that the tetrapod fauna of the region maintained a rather considerable structural consistency during all or much of the early Triassic time. The most representative assemblages of this age are those from the Blina Shales of Western Australia, the Arcadia Formation of Queensland and the Knocklofty Formation of Tasmania. Along with other forms, all of these assemblages include rhytidosteids and the last two contain also lydekkerinids and primitive proterosuchians related to *Proterosuchus* (Warren 1980; Camp and Banks 1978; Cosgriff 1969, 1974, 1984; Thulborn 1986; etc.). This association, and especially the lydekkerinid occurrence, provide a strong basis for correlating the units discussed with the *Lystrosaurus* Zone of South Africa. In the framework of the standard marine scale, they are currently assigned by different authors to either level from the Griesbachian (Lower Induan) to Smithian (Lower Olenekian) (Cosgriff 1984).

The evidence derived from those tetrapod groups, enabling a direct comparison with the marine units, is also somewhat vague. The rhytidosteids which are widely recorded from outside of Australia are known mainly from the Lower Olenekian extending nowhere over this level

(Shishkin and Vavilov 1985) while the lydekkerinids are restricted to the Induan in Europe and Greenland (Shishkin 1980). On the other hand, the capitosaurid *Parotosuchus*, described from the Arcadia Formation and the Blina Shales (Warren 1980), is indicative of the Spathian (Upper Olenekian) in Europe (Lozovsky and Shishkin 1974). Such a dating might be further supported by the presumable occurrence of the primitive plagiosaurid in the Arcadia assemblage (Warren 1985), basing on the stratigraphic position of the earliest record of this group in East Europe (Shishkin 1967, 1985). The simplest way to explain this mixing up of the distinctly dated groups in the Australian assemblages is that the bulk of the *Lystrosaurus* fauna had lived in Gondwana during the whole early Triassic. In this case it would be contemporary to both successive faunas of the proterosuchian epoch in East Europe.

Still more uncertain seems the dating of other amphibian finds from Australia. The Gosford Formation of the New South Wales ranged by palynologists (Evans 1963) from the Lower to the base of the Middle Triassic yields the larval brachyopid *Platycepsion* ("*Blinasaurus*") which is hardly comparable with the true *Blinasaurus* from the Blina Shales and the Knocklofty Formation, in contrast to interpretation by Cosgriff (1969, 1973, 1974). The accompanying "*Parotosaurus*" (Cosgriff 1972) is a juvenile capitosauroid whose generic allocation is far from clear. The younger tetrapod finds from the Triassic of the New South Wales are the capitosaurid *Subcyclotosaurus* (the Hawkesbury Formation) and the association of *Paracyclotosaurus* with the presumable brachyopid *Noto-brachyops* (the Ashfield Beds of the Wianamatta Formation). The evidence that these forms are Late Triassic in age (Cosgriff 1973) is not too strong although their evolutionary level does not exclude such a possibility.

#### DISCUSSION

The above survey shows that the sequence of the principal biotic replacement established for Europe (the proterosuchian, kannemeyeroid and dinosaur epoches) may be followed more or less clearly over other continents as well in spite of regional modifications caused by environmental and taphonomic factors. The guide elements of the earlier epoch, the proterosuchians, are known from nearly all of the sufficiently diversified Scythian faunas including even those profoundly dominated by amphibians (as it is the case for Australia). Among the latter, either lydekkerinids or trematosaurids and the early capitosaurids are most common everywhere. Although the proterosuchians still survived during the next succeeding epoch they lost their role of the leading archosaur group having been displaced by pseudosuchians. Similarly, the kannemeyeroids



appeared and became widely distributed over the world by the middle biotic epoch but later on (by Carnian) were reduced in abundance and variety, particularly in Laurasia. The dinosaurs undoubtedly begun to expand as early as the Carnian (Galton 1985; Benton 1986) and came to dominance towards the second half of the later biotic epoch.

The proposed triple division of the Triassic tetrapod history is rather distinct from that of Romer (1970a) who envisaged it as a sequence of the therapsid (A), the rhynchosaur-gomphodont (B) and the dinosaur (C) faunal epoches. The most obvious shortcoming of this scheme was the assignment of the rhynchosaur expansion to the middle epoch whereas actually it had proceeded mainly by the beginning of the Late Triassic (Chatterjee 1969, 1980; Ochev 1979; Benton 1983). Another point to be concerned, which is still accepted by most authors but rejected in this paper, is the idea of the *Lystrosaurus* and *Cynognathus* assemblages as the reference sequence for the early Triassic biotic epoch. As it has been shown above, this would mean both an artificial integration of the units pertaining to the proterosuchian and kannemeyeroïd epoch respectively and, on the other hand, a hardly acceptable dating of the *Cynognathus* Zone.

Another approach to interpretation of the faunal changes during the Triassic put forward by Anderson and Cruickshank (1978) is generalizing them in terms of the spatially restricted ecological complexes ("empires"). Of these, the lowland succession, including in ascending order the Lystrosaurid, the Kannemeyeriid/Diademodontid and the Plateosaurid/Melanosaurid Empires is thought to be most fully recorded. The two former ones are ranged as the Griesbachian and the Late Spathian (Anisian?) to Middle Norian respectively, and the latter as the Middle Norian to Rhaetian (*l.c.*, cf. p. 19, Chart 2.1). According to the modification by Benton (1983), two ecologically different successions of the lowland "empires" should be detected, corresponding principally (but not exactly) to the Gondwana and Laurasia supercontinents. The southern one includes, again, the Lystrosaurid Empire and the equivalents of two succeeding complexes of Anderson and Cruickshank (the Rhynchosaur/Diademontoid and the Prosauropod Empires), the latter being limited to the Rhaetian. The northern complexes are the Capitosaurid/Mastodonsaurid (Scythian to Ladinian), the Metoposaur/Phytosaur (Carnian to Middle Norian) and the equivalent of the Prosauropod Empire which is believed to have arisen here earlier than in Gondwana.

It seems rather obvious that these generalizations emphasizing the local environmental differences could hardly elucidate the most uniform events of the faunal evolution. Besides, in the case of Benton's concept the picture becomes still more complicated by the range overlap between the successive members of the alternative sequences and particularly by

mixing up the components of the contemporary empires in some areas (for example, in the Late Triassic of India).

Some other points of these schemes deserve more detailed comment. The dating of the early and the middle Empires accepted there implies the total lack of faunal documentation for the lowland facies of the Middle Scythian and thereby a rather uncertain position of the northern Neorhachitome fauna which either remains beyond any standard sequence (Anderson and Cruickshank 1978) or becomes arbitrarily included into the Middle Empire (Benton 1983: 35). A similar uncertainty emerges for the Australian assemblages. The principle of demarcation between the early and middle Empires does not seem clearly defined, for in both variants of the scheme, the northern *Parotosuchus* fauna is assigned to the middle Empire despite the absence of any marker group peculiar to the latter.

Much confusion with respect to dating and interrelationships of the concerned faunas has been brought by the zonal division of the Triassic faunal sequence proposed by Cooper (1982). Cooper's *Kannemeyeria* Zone includes in fact a great number of the pre-Spathian assemblages devoid of kannemeyeroids, i.e. those of East Europe (Neorhachitome fauna), Greenland, Spitzbergen, Madagascar, Australia and Tasmania and implies equating them with the much younger *Cynognathus* assemblage. The succeeding *Tetragonias* Zone is actually of mixture of the advanced Middle Triassic faunas (like that of Manda) with the antedating *Cynognathus* assemblage equivalents (Puesto Viejo, Rio Mendoza) and the still earlier (Spathian) assemblage of the Buntsandstein.

Turning to the global correlations founded above, a few concluding remarks can be made. The evolution of the Triassic tetrapod faunas appears to display a maximum of regional differences by its early phases and a tendency to a more uniform structure towards the end of the period. This change can influence to some extent the approach to correlation of the particular faunas which turns out to depend on their actual age. For the later assemblage of similar age, their contemporaneity may be often established rather safely (albeit roughly) on the basis of a single one or a few common or closely related genera, even without the extensive knowledge of the composition of the assemblage compared and their position against the biotic epoch sequence. This may be demonstrated by correlations based on such genera as *Cynognathus*, the plesiosaur *Palaeorhinus*, the rhynchosaurs *Hyperodapedon* (= *Paradapedon*?) and its relative *Scaphonyx*, etc.

But the earlier are the faunas to which this approach is applied, the more risky it becomes comparing the distant areas due to differences in the time range and tempos of evolution which are often shown by the same common groups. For instance, a close similarity of the Middle Triassic brachyopid *Batrachosuchus* from East Africa and *Batracho-*

*suchoides* from the Lower Triassic of Europe could not justify equating their respective faunas (belonging actually to the different biotic epoches). A similar difficulty appears to arise if lydekkerinids are used for correlation, as they did not outlast the Indusan in Europe but probably did so in Australia (the Arcadia assemblage). Under such conditions, the data on the structure of the faunas containing the forms compared do increase in importance.

On the other hand, the early phases of the Triassic were peculiar by a variety of the short-lived "evolutionary experiments" which gave rise to a number of the aberrant groups or genera of limited range. In contrast to a general rule just deduced, the forms of this sort are thought to provide a reliable basis for the distant correlation. The labyrinthodonts *Tupilakosaurus* and *Eocyclotosaurus* (from the Induan and Anisian respectively) may be quoted as examples here.

The effectiveness of the evolutionary level analysis of the related genera as a means of their relative dating is also variable and depends most obviously on the scale of comparison. In general, it seems more satisfactory when the forms well-separated in time are compared as it is evidenced, for instance, by the rhynchosaur succession fitting in the kannemeyeroïd and dinosaur epoches (Benton 1983). On the contrary, those allied forms being of the roughly comparable age but coming from the distant areas may sometimes display the evolutionary difference which does not reflect their actual stratigraphic relation (as it is probably demonstrated by lydekkerinids from East Europe and Tasmania; Cosgriff 1974; Shishkin 1980).

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#### ZASADY GLOBALNEJ KORELACJI TRIASU KONTYNENTALNEGO NA PODSTAWIE TETRAPODA

##### *Streszczenie*

Historia triasowych kręgowców lądowych na Ziemi obejmuje trzy kolejne epoki: epokę proterozuchów, kannemajeroideów i dinozaurów. Dwie pierwsze są reprezentowane przez regionalną sekwencję faunistyczną we wschodniej Europie. Epoka proterosuchów obejmuje tu faunę *Neorhachitomi* i faunę *Parotosuchus*. Pierwsza z nich koreluje się bezpośrednio z indem i dolnym olenekiem, druga — z górnym olenekiem (spat). Fauny *Eryosuchus* i *Mastodonsaurus* epoki kannemajeroideów we wschodniej Europie są środkowotriasowe i odpowiadają kolejno wapieniowi muszlowemu i Lettenkohle. W pracy podano dowody, że zastępowanie faun epok proterozuchów i kannemajeroideów nastąpiło równocześnie w Laurazji i na Gondwanie. To wskazuje, że zona *Cynognathus* w południowej Afryce i jej ekwiwalenty w Ameryce Południowej są środkowotriasowe. Przedstawiono sugestię, że większość fauny *Lystrosaurus* na Gondwanie obejmuje większą część, lub cały wczesny trias.