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by Saswati Bandyopadhyay^{1*} and Sanghamitra Ray²

Gondwana Vertebrate Faunas of India: Their Diversity and **Intercontinental Relationships**

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The twelve Gondwanan stratigraphic horizons of India have vielded varied vertebrate fossils. The oldest fossil record is the Endothiodon-dominated multitaxic Kundaram fauna, which correlates the Kundaram Formation with several other coeval Late Permian horizons of South Africa, Zambia, Tanzania, Mozambique, Malawi, Madagascar and Brazil. The Permian-Triassic transition in India is marked by distinct taxonomic shift and faunal characteristics and represented by small-sized holdover fauna of the Early Triassic Panchet and Kamthi fauna. The Middle and Late Triassic saw extensive radiations of the indigenous and living faunas in the form of new temnospondyls, varied archosauromorphs, the basal dinosaurs, non-mammalian cynodonts and mammaliaforms. All the Triassic Gondwanan horizons of India can be correlated with other horizons around the world, resulting in precise biostratigraphic correlation. The Triassic-Jurassic transition in India show marked biotic turnover, which may have resulted from global warming and volcanism. On a Pangaean landscape, the Indian Gondwanan vertebrate assemblages reflect major transformations in vertebrate evolution, global faunal transitions, and constitute important biostratigraphic markers.

Introduction

The Late Palaeozoic terrestrial communities were dominated by the stem-amphibians (temnospondyls) and non-mammalian synapsids, whereas the diapsids remained a minor component (Padian and Sues, 2015). The best known groups were the aquatic mesosaurs, lizardlike millerosaurs, procolophonids and large pareiasaurs. Mesozoic is the time when the species richness started to increase globally as well as locally with the appearance of new genera and early radiation of

many extant lineages, producing highly diverse terrestrial vertebrates in the vacant niches created throughout the world due to the end-Permian extinction event. Diapsids diversified rapidly by the Middle Triassic in to many communities of continental tetrapods, whereas the non-mammalian synapsids became a minor components for the remainder of the Mesozoic Era. The Gondwana basins of peninsular India (Fig. 1A) aptly exemplify the diverse vertebrate faunas found from the Late Palaeozoic and Mesozoic. During the last few decades much emphasis was given on explorations and excavations of vertebrate fossils in these basins which have yielded many new fossil vertebrates, significant both in numbers and diversity of genera, and providing information on their taphonomy, taxonomy, phylogeny, evolutionary history, palaeobiology, palaeoecology and palaeobiogeography. There are at least twelve Gondwanan stratigraphic horizons (Fig. 1B), which have yielded varied vertebrate fossils. In the current work, we review these vertebrate fossils from two perspectives. We give a comprehensive account of these fossils, their occurrences and taxonomy, followed by their global correlation and biostratigraphic implications. The study highlights several waves of faunal replacements, especially at the Permian-Triassic and Triassic-Jurassic boundaries.

Gondwana Basins of India

The Gondwana deposits of India mark the resumption of sedimentation during the Permo-Carboniferous time after a long gap since the Proterozoic, and were deposited in glacial, fluvioglacial, fluviatile and lacustrine conditions. The age of these sediments ranges from the Late Carboniferous (ca. 290 Ma) to Middle Jurassic, as separation of the Indian plate from the Gondwana landmass was initiated during the onset of the Late Jurassic (ca. 167 Ma, Chatterjee et al., 2017). The Gondwana sediments accumulated in a number of isolated intracratonic basins of peninsular India bounded by faults developed along Precambrian lineaments during deposition. The basins subsided between normal faults, accommodating the Gondwana successions of 1-4 km in thickness (Veevers and Tewari, 1995). There are four major intracratonic basins - the Pranhita-Godavari (henceforth P-G Basin), Satpura, Son-Mahanadi and Damodar (Fig. 1A) - that document the thick Gondwana Supergroup, which may be subdivided into a Lower Gondwana Group characterized by the Palaeozoic





Figure 1 A, Gondwana basins of peninsular India (after Bandyopadhyay, 1999); B, Generalized Gondwana stratigraphy showing the fossilbearing horizons in bold (after Bandyopadhyay and Sengupta, 2006; Mukherjee et al., 2012; Ray 2015); C, Geological map of the Pranhita-Godavari Basin (after Kutty et al., 1987; Ray, 1997).

Glossopteris-Gangamopteris flora and an Upper Gondwana Group dominated by the Mesozoic *Dicroidium-Lepidopteris-Ptilophyllum* flora (Cotter and De, 1917; Robinson, 1970; Pascoe, 1975; Mukhopadhyay et al., 2010). The Lower Gondwana succession in most of the basins shows uniform lithological features, starting with the glacio-fluvial Talchir Formation and followed by the coal-bearing Barakar Formation (Fig. 1B). The Upper Gondwana succession of these basins, however, differs considerably and the formations are defined on the basis of distinctive lithology, fossil flora and fauna (Fig. 1B).

Among the four Gondwana basins of India (Fig. 1A), the Gondwana succession of the P-G Basin occurs in a narrow, rectilinear half-graben (400 km long and 75 km wide) trending NNW-SSE (330°-150°) and bordered on both sides by the Precambrian rocks (Fig. 1C). The overall dip of this half-graben basin, which was formed with the hanging-wall block lying to its west (Biswas, 2003; Chakraborty et al., 2003), is 5°-12° towards NE (Chakraborty et al., 2003) and the general palaeocurrent direction is to the north (Sengupta, 1970). Seven vertebrate-bearing horizons have been identified from this basin, which have yielded highly diverse vertebrate remains (Bandyopadhyay, 1999). These include the Late Permian Kundaram Formation, and different Triassic horizons such as the Kamthi, Yerrapalli, Maleri and Lower Dharmaram formations, and the Jurassic Upper Dharmaram and Kota formations (Bandyopadhyay, 1999, 2011). The Maleri Formation has two vertebrate assemblages, which have led to a biochronological subdivision into lower (Carnian) and upper (Norian) horizons (Kutty and Sengupta 1989).

The westernmost Satpura basin (Fig. 2A) is rhomboidal in outline, and is about 200 km long and 60 km wide. The longer sides are marked

by the ENE–WSW-trending Son-Narmada (south) and Tapti (north) faults. This basin is a pull-apart basin and developed due to the extension related to strike-slip movements along these two faults (Chakraborty et al., 2003). The regional strike of the basin fill is ENE–WSW and the regional formation dip is ca. 5° to the north. The Gondwana succession (ca. 4 km in thickness) consists of siliciclastic sediments and ranges in age from Early Carboniferous to the Middle Triassic (Crookshank, 1936; Pascoe, 1975; Robinson, 1970; Bandyopadhyay and Sengupta, 1999). There are only two vertebrate-bearing horizons in this basin: the Late Permian Bijori Formation and the Middle Triassic Denwa Formation (Lydekker, 1885a, b; Bandyopadhyay and Sengupta, 1999).

In eastern India along the E–W trending Damodar Basin (Fig. 1A), several isolated basins occur, which are of similar morphology and structural characteristics. These are the Karanpura and Bokaro basins along with the small outliers of Auranga and Hutar, Jharia Basin and Raniganj Basin from west to east. The basins are all rhombic, fault-bound with numerous intrabasinal faults at high angles to the bounding faults along their longer sides (Chakraborty et al., 2003). Of these basins, the Raniganj Basin is a fault-controlled subsidence basin which has produced vertebrate remains. It is rhomboidal in outline (70 km long and 20 km wide), relatively long in WNW–ESE direction with low (5°-7°) dip towards south (Fig. 2B). The Damodar Basin has a thick succession (ca. 3 km thick) of fluvioglacial, fluvial and lacustrine sediments, though vertebrate fossils are known from only one horizon, the Early Triassic Panchet Formation (Fig. 1B, 2B).

The Son-Mahanadi, centrally positioned in peninsular India (Fig. 1A), is a composite basin and comprises three sub-basins, namely



Figure 2. Geological maps of A, Satpura Basin (after Sengupta et al., 2016); B, Damodar Basin (after Ray, 2005); C, Rewa Basin (after Mukherjee et al., 2012).

the Rewa Basin in the north (Fig. 2C, inset), the centrally-located Hasdo-Arand Basin, and the Mahanadi Basin in the south. The Rewa Basin is bounded by the Malwa ridge in the north and by the Manendragarh-Pratapur ridge in the south (Chakrabortv et al., 2003). The basin is rhomboidal in outline and extends in an essentially ENE-WSW direction (400 km x 150 km). The overall attitude of the basinfill strata is less than 15° to the north. This basin is considered a fault-controlled subsidence basin (Chakraborty et al., 2003), and is characterized by a thick and continuous Triassic succession (Mukherjee et al., 2012). The Triassic succession is subdivided into the Pali Formation at the base, followed successively by an arenaceous Karki Formation and a mud-dominated Tiki Formation (Mukherjee et al., 2012; Fig. 1B). Of these, the Tiki Formation (Fig. 2C) has yielded a rich Late Triassic vertebrate fauna (Datta and Das, 1996; Datta, 2004, 2005; Prasad et al., 2008; Ray et al., 2016; Bhat et al., 2018a, b; Datta et al., 2019).

Gondwana Vertebrate Faunas

Permian Vertebrate Fauna

Faunal characteristics

In India, Permian vertebrates have a poor representation and are known from two distinct horizons, namely the Vihi (*Gangamopteris*) beds of the Mamal Formation of Kashmir (Bandyopadhyay, 1999) and the Kundaram Formation of the P-G Basin (Kutty, 1972; Ray, 1999, 2001). The Kashmir fauna is characterized by several palaeoniscoid fishes and archegosauroid temnospondyls (Woodward, 1905; Tripathi, 1962), the details of which were given by Bandyopadhyay (1999). Since there has been no update on the already available information, the faunal details are not repeated here.

On the other hand, the Kundaram Formation of P-G Basin has yielded a Late Permian multitaxic tetrapod fauna where the dominant component is the dicynodonts. The non-dicynodont members include a small captorhinid reptile (Kutty, 1972) and a medium-sized gorgonopsian (Ray and Bandyopadhyay, 2003). The dicynodont assemblage includes two species of the genus Endothiodon (E. mahalanobisi and E. uniseries), Dicynodontoides (= 'Kingoria'), Pristerodon, Oudenodon and Sauroscaptor (Fig.3A-B; Ray, 2000, 2001; Ray and Bandyopadhyay, 2003; Kammerer et al., 2016). The fauna is mostly represented by complete and partial skulls and lower jaws, and shows a preponderance of Endothiodon known from about 30 individuals (Ray, 1999; Ray and Bandyopadhyay, 2003). This skullonly accumulation, encrusted with thick iron-rich matrix and collected from overbank fines, is a lag deposit and has been attributed to prolonged subaerial exposure prior to burial, resulting in disarticulation and winnowing out of the postcrania by water flow as the heavier skulls resisted transportation and were subsequently buried near the site of death (Ray and Bandyopadhyay, 2003).

Intercontinental relationships

The Late Permian palaeogeography encompassed three large continental masses that are principally distributed at the mid-latitudes, namely the Gondwana, Laurasia and Siberia, joined together to form the supercontinent Pangaea (Bernardi et al., 2017). Well documented Late Permian tetrapod ecosystems are known from these landmasses, where the tetrapod associations were structured and provincialized at



Figure 3. A-B, Sauroscaptor tharavati Kammerer et al. (2016). Skull of a small dicynodont from the Kundaram Formation of India in A, dorsal and B, ventral views.

high taxonomic levels (Bernardi et al., 2017). Of these, the Permo-Triassic Beaufort Group of the Karoo Basin in South Africa documents a rich tetrapod fossil record, which has resulted in its biostratigraphic subdivisions (Rubidge, 1995; Smith et al., 2012) with global applicability. Of the six Assemblage Zones (AZ) Pristerodon and Endothiodon appeared first in the Pristerognathus AZ, proliferated in the Tropidostoma AZ and persisted as a rare member in the Cistecephalus AZ (Rubidge, 1995). In addition, the Pristerognathus AZ contains the small dicynodont Diictodon, which constitutes about 85% of the total fossils found. It decreases to about 40% in the Tropidostoma AZ (Rubidge, 1995), where Rhachiocephalus and Endothiodon (E. miseries, E. bathystoma) constitute 10-30% and 5%, respectively. Similarly, the fossil fauna of the Cistecephalus AZ is composed of Diictodon (50%) followed by Oudenodon (20%), Cistecephalus (10%), Pristerodon (5%), Emydops (5%), Aulacephalodon (5%), Rhachiocephalus and Endothiodon (less than 2%, Rubidge, 1995).

There are several other Endothiodon-bearing horizons in Africa, which are analogous to the Karoo environment and are found in Zimbabwe, Mozambique, Malawi, Zambia and Tanzania (King, 1992). In Zambia, the Lopingian is represented by the Upper Madumabisa Mudstone Formation in the Luangwa Basin, from which a single assemblage of 14 dicynodont taxa is known and correlated with the Cistecephalus AZ of South Africa (King, 1992; Angielcyzk et al., 2014; Sidor et al., 2014). The Late Permian tetrapod fossils are preserved in the Ruhuhu and Usili formations of the Ruhuhu Basin of Tanzania, where the tetrapods occur at multiple stratigraphic horizons in each formation (Angielczyk et al., 2014). The Usili horizons and the uppermost Ruhuhu horizon contain a single faunal assemblage dominated by dicynodonts consisting of endothiodonts, emydopoids, cryptodonts, and dicynodontoids (52%), followed by gorgonopsians, therocephalians, cynodonts and notably abundant biarmosuchians (35%), pareiasaurs (5.5%) and temnospondyls (6.6%). Bernardi et al. (2017) suggested that these horizons may be correlated with the upper Cistecephalus and/or lower Daptocephalus AZs of the Karoo Basin.

Endothiodon is also known from the K5 horizon of the Metangula

Graben, Mozambique along with an endemic kingoriid dicynodont *Niassodon* and a probable *Oudenodon* (Castanhinha et al., 2013). Based on the presence of *Endothiodon* and *Oudenodon*, the latter making its first appearance in the *Tropidostoma* AZ of South Africa, K5 is correlated broadly with the *Tropidostoma* and *Cistecephalus* AZs (Castanhinha et al., 2013). In addition, *Endothiodon*-bearing strata are also known from the Chiweta beds of Malawi (Frobisch, 2009; Bernardi et al., 2017). The Lower Sakamena Formation of Madagascar is known for its richness in the Late Permian fossils, which are characterized by the diapsids (Smith, 2000). Mazin and King (1991) described a dicynodont taxon, *Oudenodon sakamenenis* from the upper part of Lower Sakamena Formation. Though long-ranging, this genus is common in the *Cistecephalus* and *Dicynodon* AZs of South Africa suggesting a probable correlation.

Apart from Africa and India, a rich Late Permian fauna is known from the Rio do Rasto Formation of the Paraná Basin, Brazil (Cisneros and Abdala, 2005; Benardi et al., 2017). The Rio do Rasto Formation of the Paraná Basin has produced three local faunas containing vertebrates– the Aceguá, Posto Queimado and Serra do Cadeado (Barberena et al., 1991). Of these, the Serra do Cadeado local fauna consists of *Endothiodon* (Barberena et al., 1975) and long-snouted rhinesuchids, including *Australerpeton cosgriffi*, suggesting that the Serra do Cadeado fauna can be loosely correlated with *Pristerognathus, Tropidostoma* and *Cistecephalus* AZs.

A close similarity of the Kundaram vertebrate fauna with that of the *Tropidostoma* and/or *Cistecephalus* (AZ) was noted based on their dicynodont-content (Ray, 1999). Subsequent works by several authors have shown that *Endothiodon* dominates in the Kundaram fauna; the latter containing the long-ranging *Pristerodon*, *Oudenodon* and a cistecephalid *Sauroscaptor* (Ray, 2001; Kammerer et al., 2016), with a gorgonopsian (Ray and Bandyopadhyay, 2003) and a captorhinid (Kutty, 1972). Based on this dicynodont-rich fossil content, the Kundaram Formation may be correlated with the *Tropidostoma* and lower *Cistecephalus* AZs of South Africa, and several other *Endothiodon*-bearing African strata (Fig. 4). These include the upper Madumabisa Mudstones of Zambia, Ruhuhu and Kawinga formations of Tanzania, K5 horizon of Mozambique, Chiweta Bed of Malawi. In

		ł	Russia		Brazil	South Africa	Mozam- bique	Malawi	Zambia	a	Tanzania	Mada- gascar	India										
Ľ	⊑ Chnx			R		Dicynodon					Kawinga (K6)	Lower											
ngia			Vyazniki	0		Cistecephalus	K5	Chiwata			or Usili	Sakamena											
Lopi	· do log log log log log log log log log lo		Sokolki	d	Morro Pelado	Tropidostoma	кə	Bed	Madu-				Kundaram										
	Cani	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria	Tataria		R		Pristero- gnathus*			bisa Mud-		Ruhuhu (K5)		
upian	tanian		llinskoe	a s t	Serrinha	Tapino- cephalus			Fm.	L													
Gualal	Wordian		Kotelnich	0		Eodicynodon																	
	Roadian	к	azanian																				

Figure 4. Correlation of the Upper Permian vertebrate-bearing horizons around the world (shaded in grey). Middle-Upper Permian time scale follows Gradstein et al. (2012). Abbreviation: Chnx, Changhsingian; Sources of information: Rubidge (1995), Ray (1999), Cisneros and Abdala (2005), Smith et al. (2012), Bernardi et al. (2017).

addition, the Kundaram Formation may be correlated with the Lower Sakamena Formation of Madagascar and the Morro Pelado member of the Rio do Rasto Formation of Brazil. Hence, an early Lopingian (Wuchiapingian) age is suggested for the Kundaram vertebrate fauna.

Triassic Vertebrate Faunas

The largest and most devastating mass extinction event took place at the end of the Permian period when 70% of marine genera and 70-80% of the terrestrial families became extinct (Dineen et al., 2014). The Triassic period (252.2-201.3 my; Gradstein et al., 2012) is characterized by extraordinary changes in terms of vegetation due to different climatic conditions, two major extinction events and advancement in vertebrate evolution (Sues and Fraser, 2010). The typical hot and arid climate of the Late Permian continued at the beginning of the Triassic but gradually the period witnessed fairly moist and hot climate of monsoon type with an alternation of wet and dry seasons (Robinson, 1970; Preto et al., 2010; Sues and Fraser, 2010). The long 50 million year Triassic period started with impoverished terrestrial vertebrate diversity when the competition for niche space was low because of low beta-diversity which gradually increased with subsequent origination, speciation and interaction between species resulting in diversification (Hoffmann et al., 2013; Hautmann, 2014). The geologically ephemeral Early Triassic fauna was replaced by a novel Middle Triassic community with renewed incumbency (Roopnarine, 2018) but low level of cosmopolitanism (Sahney and Benton, 2008). The period ended with a highly diverse vertebrate fauna that included varied temnospondyls, lepidosaurs, crocodilians, non-avian dinosaurs and early mammals, thus restoring the terrestrial tetrapod community and setting the stage for the modern terrestrial ecosystem (Fraser, 2006; Sues and Fraser, 2010). The Late Triassic thus may be considered as a transitional period between ancient and modern terrestrial ecosystems.

Three general continental tetrapod faunas dominated the Triassic. These faunas comprised the 'Palaeozoic holdovers', which was the Early Triassic tetrapod assemblage that survived the end-Permian extinction to proliferate during the Triassic, the 'indigenous' Triassic fauna, which appeared and became extinct during the Late Triassic, and the 'living' fauna, which appeared during the Late Triassic and are still continuing today. This latter group consists of the dinosaurs (including birds), crocodylians, turtles, lepidosaurs and several extant groups of amphibians (Romer, 1966; Padian and Sues, 2015). Representative fossils of these groups are found in the Indian scenario, the details of which are discussed in the following section.

Early Triassic

There are two Early Triassic horizons bearing representative vertebrate fossils in India. These include the Panchet Formation of the Damodar basin and the Kamthi Formation of the P-G Basin (Fig. 1B). Of these, the Panchet Formation (Fig. 2B), comprising essentially siliciclastic sediments, has yielded various vertebrate remains in the sandstone and shale. The ichthyofaunal assemblage includes numerous scales, teeth and tooth plates of actinopterygians, dipnoans and chondrichthyans suggesting lack of endemism (Gupta, 2009). This formation also includes several temnospondyls, dicynodonts, diapsids and cynodonts (Table 1). The temnospondyls are represented by the trematosaurids *Indolyrocephalus, Gonioglyptus*, a rhytidosteid *Indobrachyops*, a lydekkerinid, *Lydekkerina*, a

lapillopsid *Manubrantlia*, a plagiosaurid *Capulomala*, a brachyopid *Pachygonia*, a probable tupilakosaurid *Tupilakosaurus* sp., and an indeterminate benthosuchid (Bandyopadhyay, 1999, 2011; Warren et al., 2009; D. P. Sengupta, pers comm.). The Panchet fauna also includes possibly three species of the dicynodont, *Lystrosaurus* (Tripathi and Satsangi, 1963; Ray, 2005; Gupta and Das, 2011), two cynodonts, *Thrinxodon* and *Panchetocynodon* (Satsangi, 1987; Das and Gupta, 2012) and the diapsid *Proterosuchus* (Huxley, 1865; Bandyopadhyay, 1999, 2011; Table 1).

The other Early Triassic vertebrate-bearing horizon is the Kamthi Formation of the P-G Basin. This formation has purple siltstone and ferruginous sandstones, which are pebbly in places. The Kamthi siltstone has yielded numerous small, articulated but poorly preserved, skeletons (Fig. 5A-B), which were identified as a dicynodont (Bandyopadhyay and Sengupta, 2006). Although the skulls are mostly broken or distorted, these are large with flaring posterior ends, especially the squamosals. The postcranial skeletons are, in comparison well preserved and articulated. The Kamthi dicynodont is characterized by a robust humerus with expanded ends, which is smaller than the associated femur, and the presence of two U-shaped deep notches on the dorsal margin of the iliac blade (Fig. 5B). Such notched iliac border resulting in three possible origination sites for the ilio-femoralis muscle is seen only in the dicynodont Lystrosaurus (Ray, 2006). Presence of this unique feature suggests that the Kamthi dicynodont was Lystrosaurus, though other vertebrate fossils are yet



Figure 5A-B, Lystrosaurus sp. Articulated skeletons found on the purple siltstone of the Kamthi Formation.

	Panchet	Yerrapalli	Denwa
PISCES			
Acrolepidae	Indeterminate genus	-	-
Perleididae	Indeterminate genus	-	-
Chondrichthyes	Indeterminate genus	-	-
Ceratodontidae	Indeterminate genus	Ceratodus sp.	Ceratodus sp.
Saurichthyformes	-	Saurichthys sp.	
AMPHIBIA			
Rhytidosteidae	Indobrachyops panchetensis	-	-
Trematosauridae	Indolyrocephalus huxleyi	-	Lonchorhynchine indet.
	Gonioglyptus fragilis		
	Gonioglyptus longirostris		
Lapillopsidae	Manubrantlia khaki	-	-
Lydekkerinidae	Lydekkerina huxleyi		
Plagiosauridae	Capulomala panchetensis	-	
Brachyopidae	?Pachygonia incurvata	-	Undescribed
Benthosuchidae	?benthosuchid	-	-
Tupilakosauridae	Tupilakosaurus sp.	-	-
Mastodonosauridae	-	Parotosuchus rajareddyi	-
Capitosauroidea	-	-	Paracyclotosaurus
			crookshanki Chaminin damani
DIA DEIDA			Cherninia denwai
Proterosuchidae	Proterosuchus (Chasmatosaurus	-	-
	Ankistrodon) indicus		
Rhynchosauridae	-	Mesodapedon kuttyi	Undescribed
Allokotosauria	-	Pamelaria dolichotrachlea	Shringasaurus indicus
Erythrosuchidae	-	Erythrosuchus sp.	
Aphanosauria	-	Yarasuchus deccanensis	-
SYNAPSIDA			
Lystrosauridae	Lystrosaurus murrayi	-	-
	L. cf. declivis, L. cf. curvatus	-	-
Kannemeyeriiform	-	Wadiasaurus indicus	Undescribed taxa
Stahleckeriidae	-	Rechnisaurus cristarhynchus	-
Thrinaxodontidae	Thrinaxodon bengalensis	-	-
Brasilodontidae	Panchetocynodon		
	damodarensis	-	-
Trirachodontidae	-	Trirachodontidae indet.	-

Table 1. Lower and Middle Triassic vertebrate faunas of India. Sources of information: Tripathi and Satsangi (1963), Bandyopadhyay (2011), Ray (2005), Bandyopadhyay and Sengupta (2006), Gupta and Das (2011), Das and Gupta (2012), Sengupta et al. (2017), D. P. Sengupta pers.comm. (2018)

to be recovered from the formation. In addition, the temnospondyl *Brachyops laticeps* is known from the upper part of the Kamthi Formation or the 'Mangli' beds' (Owen, 1855).

Middle Triassic

The Yerrapalli Formation of the P-G Basin and the Denwa Formation of the Satpura Basin (Figs 1B–C, 2A) are the major Middle Triassic vertebrate-bearing horizons of India (Crookshank, 1936; Jain et al., 1964), though fragmentary remains of a dicynodont and temnospondyl are known from the Bhimaram Formation (Kutty et al., 1987). The strata of the Yerrapalli Formation comprise red to violet mudstone alternating with quartzose sandstone, with mudstone being fossil-rich. The vertebrate assemblage (Table 1) consists of the ceratodontid *Ceratodus*, the saurichthyform *Saurichthys*, the capitosaur *Parotosuchus*, the stenaulorhynchine rhynchosaur *Mesodapedon*, the allokotosaur *Pamelaria*, the erythrosuchid *Erythrosuchus*, the aphanosaur *Yarasuchus*, two kannemeyeriiform dicynodonts (*Wadiasaurus* and *Rechnisaurus*), and a trirachodontid.

The Denwa Formation of the Satpura Basin is the other wellknown Middle Triassic vertebrate-bearing horizon of India. On the basis of lithology, Maulik et al. (2000) divided the formation into lower and upper parts. The lower Denwa comprises multistoried, sheet-like medium-fine grained sandstone bodies interleaved with red mudstones, while the upper Denwa is a mudstone-dominated unit characterized by layers of ribbon-shaped channel-fill bodies and sandy to heterolithic sheet sandstones encased within the mudstones. The vertebrate assemblage (Table 1) includes the ceratodontid *Ceratodus*, the capitosaurs *Paracyclotosaurus*, *Cherninia*, and three indeterminate taxa, the undescribed brachyopid, the lonchorhynchine trematosaurid, an undescribed rhynchosaur, and various medium–large dicynodonts (Mukherjee and Sengupta, 1998; Bandyopadhyay and Sengupta, 1999; Mukherjee et al., 2019). Recently the horned allokotosaur *Shringasaurus* (Fig. 6A–B) has been described from this horizon (Sengupta et al., 2017). This is the only known horned Triassic reptile to date.

Late Triassic

Three Late Triassic horizons of India contain distinct vertebrate assemblages — the Maleri and the lower Dharmaram formations of the P-G Basin (Table 2) and the Tiki Formation of the Rewa Basin (Table 3). The Maleri Formation is represented by a mudstone-dominated, nearly 400-m-thick fluvial succession deposited under a semi-arid climate (Sarkar, 1988) and may be subdivided into two parts. The lower part (100–150 m thick) comprises vertically stacked siltstone-dominated intervals, whereas the upper part (200–300 m thick) contains multistoried, sheet sandstone, vertically separated by comparatively thicker siltstone-dominated intervals (Dasgupta and Ghosh, 2018). Numerous thin, sheet-like and lensoid bodies of cross-bedded grainstones occur at different stratigraphic levels (Dasgupta et al., 2017).

This formation has yielded two distinct vertebrate assemblages

(Kutty and Sengupta, 1989; Prasad et al., 2008; Bandyopadhyay, 2011; Chakravorti and Sengupta, 2019). The Maleri Formation encompasses 12 families, which represent 25 genera and species (Table 2), of which 12 and 13 taxa belonged to the lower and upper Maleri faunas, respectively. The lower Maleri fauna is characterized by an association of the phytosaur *Parasuchus*, the rhynchosaur *Hyperodapedon* and the metoposaurid *Panthasaurus* (Chatterjee, 1974, 1978; RoyChowdhury, 1965; Chakravorti and Sengupta, 2019). Other vertebrates comprise a ptychoceratodontid, a xenacanthid, a prolacertid (?), a yet to be described phytosaur similar to *Angistorhinus*, an aetosaur similar to *Typothorax*, an allokotosaur, a basal saurischian, and two cynodont genera (Bandyopadhyay, 2011; Novas et al., 2011; Nesbitt et al., 2017; Table 2).

The upper Maleri fauna, on the other hand, includes two chigutisaurids, *Kuttycephalus* and *Compsocerops* (Kutty and Sengupta, 1989), two derived phytosaurs similar to *Angistorhinus* and *Leptosuchus* (Hungerbühler et al., 2002), two dinosauromorphs (Novas et al., 2011), and a dicynodont very similar to *Stahleckeria* (Novas et al 2011; Bandyopadhyay, 2011; Table 2). This faunal assemblage occurs in a stratigraphically younger horizon, from which *Panthasaurus, Hyperodapedon, Parasuchus* and *Exaeretodon* had disappeared, suggesting that the latter is younger than the lower Maleri fauna (Kutty and Sengupta, 1989).

The Maleri Formation is overlain by the Dharmaram Formation, one of the most important stratigraphic horizons, and encompasses the Triassic-Jurassic boundary in the Indian Gondwana (Bandyopadhyay and RoyChowdhury, 1996). It has been biochronologically divided into a lower part bearing a Rhaetian fauna and an upper part yielding a Hettangian fauna (Bandyopadhyay and



Figure 6. A-B, Shringasaurus indicus Sengupta et al. (2017). A horned allokotosaur from the Denwa Formation of India as A, reconstructed skeleton; B, restored life form. Missing bones are shaded by grey.

	Lower Maleri	Upper Maleri	Lower Dharmaram
PISCES			
Ceratodontidae	Ptychoceratodus virapa	-	-
	-	P. nageswari	P. nageswari
Polyacrodontidae	Polyacrodus? contrarius	-	-
Xenacanthidae	Mooreodontus indicus	M. indicus	M. indicus
AMPHIBIA			
Metoposauridae	Panthasaurus maleriensis	-	-
Chigutisauridae	-	Compsocerops cosgriffi	-
	-	Kuttycephalus triangularis	-
DIAPSIDA			
Phytosauria	Parasuchus hislopi	cf. Leptosuchus	Nicrosaurus-like form
	Angistorhinus	Angistorhinus	-
Rhynchosauria	Hyperodapedon huxleyi	-	-
Prolacertiformes	Malerisaurus robinsonae	-	-
Aetosauria	cf. Typothorax	Aetosauria indet.	Paratypothorax-like form
	-	-	Desmatosuchus-like form
Dinosauriformes	Alwalkeria maleriensis	Gen indet. A (ISI R282)	J. asymmetrica
		Gen indet. A (284)	Sauropodomorpha indet.
		Nambalia roychowdhurii	Neotheropoda indet.
		<i>Jakiapauisaurus asymmetrica</i> Guibasauridae indet	
Discussion dentie		C. I. discontantin	
Dicynodontia		cf. Ischigualastia	-
Cynodontia	Exaeretodon statisticae Deccanodon maleriensis	-	-

Table 2. Late Triassic vertebrates from different stratigraphic horizons of the P-G Basin, India. Sources of information: Kutty and Sengupta (1989), Bandyopadhyay (1999, 2011), Prasad et al. (2008), Chakravorti and Sengupta (2019)

RoyChowdhury, 1996, Bandyopadhyay, 2016). This formation is a sandstone-dominated unit that contains subordinate amount of mudstone. The Rhaetian faunal assemblage contains 8 taxa (Table 2), comprising a ptychoceratodontid, a xenacanthid (Nath and Yadagiri, 2007; Prasad et al., 2008), a derived phytosaur similar to *Nicrosaurus*, an aetosaurid similar to *Paratypothorax* (Kutty et al 2007; Bandyopadhyay, 2011), several sauropodomorphs, and a neotheropod (Novas et al., 2011).

Another Late Triassic Gondwana horizon that is rich in varied vertebrate fossils is the Tiki Formation of the Rewa Basin (Fig. 7A-P). It has yielded a diverse fish assemblage comprising hybodontid and xenacanthid sharks, dipnoans and actinopterygians (Prasad et al., 2008; Ray et al., 2016; Bhat and Ray, 2018; Bhat et al., 2018a, b) a metoposaurid, Panthasaurus maleriensis (Sengupta, 2002; Chakravorti and Sengupta, 2019), various diapsids including the rauisuchid Tikisuchus romeri and the rhynchosaur Hyperodapedon tikiensis (Chatterjee and Mazumdar, 1987; Mukherjee and Ray, 2014). Numerous archosauriform teeth belonging to 12 distinct morphotypes have been reported from the Tiki Formation (Ray et al., 2019). These include Galtonia, Protecovasaurus, aetosaur, indeterminate archosauriforms and theropod-like forms. Recently Datta et al. (2019a) reported numerous isolated teeth of a possible leptosuchomorph-grade phytosaur. Moreover, review of the skull earlier identified as Parasuchus from the Tiki Formation (Chatterjee 1978) is found to have belonged to a a new mystriosuchine phytosaur Volcanosuchus statisticae (Datta et al. 2019b). The formation has also yielded

fragmentary remains of a saurischian dinosaur (Ray et al., 2016) and small theropod-like ungual phalanges (Rakshit et al., 2018). It may be noted that putatively the earliest lizard Tikiguania estesi (Datta and Ray, 2006) was reported from this formation. However, Hutchinson et al. (2012) questioned the provenance and geologic horizon of Tikiguania because it is almost indistinguishable from living agamids and suggested that the fossil might have come from younger horizons. As Tikiguania was extracted from the Tiki mudstones, which have yielded a rich microvertebrate fauna (Bhat, 2018; Bhat et al., 2018a, b; Bhat and Ray, 2018; Rakshit et al., 2018; Ray et al., 2019), such contamination hypothesis seems less likely (Chatterjee et al., 2017). However, unless more conclusive evidence is available, the taxon is excluded from the Tiki faunal list (Table 3). The formation has also yielded various non-mammalian cynodonts including a large traversodontid Ruberodon roychowdhurii (Ray, 2015), a small non-mammalian cynodont Rewaconodon tikiensis (Datta et al., 2004), a morganucodontid mammal Gondwanadon tapani (Datta and Das, 1996) and, one of the earliest 'nontherian' mammals Tiktherium, which is characterized by transversely expanded molar (Datta, 2005).

Triassic Intercontinental Relationships

Early Triassic Global Correlation

The Panchet fauna virtually duplicates the Early Triassic faunas



Figure 7. Vertebrates from the Late Triassic Tiki Formation of India. A-B, scattered fossils in the field; C-D, Hyperdapedon tikiensis Mukherjee and Ray (2014). Maxillary dental batteries in ventral views; E, Volcanosuchus statisticae Datta et al. (2019b). A partial skull in anterior view; F, Tikisuchus romeri Chatterjee and Mazumdar (1987). Restored skull and lower jaw; G-P, isolated teeth of G, Ptychoceratodus oldhami Bhat and Ray (2018) in ventral view; H-I, Pristrisodus tikiensis Bhat et al. (2018a) in H, labial and I, lingual views; J-O, xenacanthid, J-L, Xenacanthus jaini and M-O, Xenacanthus indicus (Bhat et al., 2018b) in labial, lingual and side views; P, an archosauriform tooth in labial view (Bhat, 2018).

of South Africa, Antarctica, Russia and China, showing similar faunal associations, and suggesting a Pangaean vertebrate assemblage (Bandyopadhyay, 2011). Although the earliest *Lystrosaurus* (*L. maccaigi*) is known from the latest Permian *Dicynodon* AZ (Smith and Ward, 2001), typical *Lystrosaurus* species including *L. murrayi* and *L. curvatus* appeared in the earliest Triassic *Lystrosaurus* AZ

(Smith et al., 2012) and hence may be correlated with the Panchet Formation. In addition, the Panchet fauna may be correlated with other *Lystrosaurus*-bearing horizons such as the Kamthi Formation of the P-G Basin, the N'tawere Formation of Zambia and the Lower Fremouw Formation of Antarctica (Fig. 8).

The Lystrosaurus - Thrinaxodon - Proterosuchus association is

Order/Family	Genus and species	Order/Family	Genus and species		
CHONDRICHTHYIS		DIAPSIDA			
Lonchididae	Lonchidion estesi	Phytosauria	Volcanosuchus statisticae		
	Lonchidion incumbens		(?)leptosuchomorph		
	Pristrisodus tikiensis	Rhynchosauria	Hyperodapedon tikiensis		
Xenacanthidae	Mooreodontus indicus	Rauisuchidae	Tikisuchus romeri		
	Mooreodontus jaini	Rhynchocephalia	Undescribed		
	Tikiodontus asymmetricus	Archosauriformes	Galtonia sp., Protecovasaurus sp., other indeterminate forms		
OSTEICHTHYIS		Dinosauriformes	Undescribed		
Ptychocerato-dontidae	Ceratodus sp.		Theropod-like(?) forms		
	Ptychoceratodus oldhami	Aetosauria	Undescribed		
Gnathorhizidae	Gnathorhiza sp.	SYNAPSIDA			
Actinopterygii	Undescribed	Cynodontia	Ruberodon roychowdhurii		
AMPHIBIA			Rewaconodon tikiensis		
Metoposauridae	Panthasaurus maleriensis	Mammaliaformes	Tikitherium copei Gondwanadon tapani		

Table 3. Vertebrate fossil assemblage of the Late Triassic Tiki Formation of the Rewa Gondwana Basin, India. Sources of information: Datta and Das (1996), Datta (2004), Mukherjee and Ray (2014), Ray et al. (2016, 2019), Bhat and Ray (2018), Bhat et al. (2018a, b), Rakshit et al. (2018), Datta et al. (2019a, b).

well known from the Lystrosaurus AZ of the Beaufort Group of South Africa and the Fremouw Formation of Antarctica (Kitching et al., 1972; Colbert and Kitching, 1977). However, the temnospondyl fauna of the Panchet Formation is more diverse as well as cosmopolitan. There are six or seven temnospondyl families in contrast to only two or three species of Lystrosaurus, a species of Proterosuchus, and two cynodont taxa although the abundance of Lystrosaurus far exceeds that of the other taxa. Based on these tetrapods, the Panchet fauna may be correlated with the Arcadia Formation of Australia, Knocklofty Formation of Tasmania, the Wordie Creek Formation of East Greenland, the Wupatki and Torrey members of the Moenkopi Formation of USA, and the Puesto Viejo and Rio Mendoza formations of Argentina. The age of the Panchet Formation is considered as Early Triassic (Induan-Early Olenekian; Cosgriff, 1984; Ray, 2005, 2015). The abundance of small Lystrosaurus specimens from the Kamthi Formation points towards correlation with the Lystrosaurus AZ of the Beaufort Group of South Africa, suggesting that the Kamthi Formation may be considered as Early Triassic in age. The specific identification of these Lystrosaurus specimens is not possible because of their fragmentary condition. A distinct time gap is envisaged between the Early Triassic Kamthi Formation and the underlying Kundaram Formation, which is Late Permian (early Lopingian, Wuchiapingian) in age (Fig. 1B).

Middle Triassic Global Correlation

With the beginning of the Triassic period, *Lystrosaurus*, became the most common tetrapod immediately after the end-Permian extinction event, and rapid turnover gave way to the archosauromorphs (Sahney and Benton, 2008). In the Pangaean scenario, the diversity of the once dominant temnospondyls and herbivorous synapsids started to decline at the beginning of the Middle Triassic and simultaneously the diapsids continued to flourish. However, the Middle Triassic continental vertebrates are comparatively less well represented because of the worldwide increase in marine conditions, especially in Laurasia (Gandin et al., 1982; Hallam, 1992). In terms of climate the Middle Triassic period was fairly hot and moist with alternate wet monsoon and dry seasons (Robinson, 1973; Tucker and Benton, 1982; Preto et al., 2010). Temnospondyl amphibians are the most common vertebrate fossils in many Middle Triassic assemblages and diverse archosauromorphs as well as archosaurs also started to flourish. The important Middle Triassic vertebrate horizons of Laurasia include the Holbrook and the Anton Chico members (Anisian) of the Moenkopi Formation in USA (Schoch et al., 2010), much of the Buntsandstein in Central Europe (Gradstein et al., 2012), the Dongus and Bukobay formations of Russia (Sennikov, 1996), Grenzbitumen-Zone of Switzerland (Röhl et al., 2001), the Otter Sandstone and the Bromsgrove Sandstone formations of United Kingdom (Milner et al., 1990), the Er-ma-ying Formation of Shanxi and Inner Mongolia (Zhang et al., 2003; Sues and Fraser, 2010; Sookias et al., 2014), and the Karamay Formation of Xinjiang, China (He et al., 2014). The most important Middle Triassic vertebrate yielding horizon in Gondwana is the Manda Formation of Tanzania (Cox, 1991; Lucas, 1998); it has produced a large number of Middle Triassic vertebrates. The other horizons are the Omingonde Formation of Namibia (Keyser, 1973; Pickford, 1995; Abdala and Smith, 2009), the N'tawere Formation of Zambia (Catuneanu et al., 2005; Rubidge, 2015), the Arcadia Formation, and the Hawkesbury and Wianamatta formations of Australia (Banks, 1978; Warren, 2012).

Jain et al. (1964) considered the age of Yerrapalli Formation as late Early Triassic or possibly early Middle Triassic. Later, with the recovery of the kannemeyeriid dicynodont (Roy Chowdhury, 1970; Bandyopadhyay, 1988a), and the stenaulorhynchine rhynchosaur (Chatterjee 1980), the formation was correlated with the Manda Formation of Tanzania, N'tawere Formation of Zambia, the Donguz Series of Russia, and the Omingonde Formation of Namibia, and an Anisian age for the Yerrapalli Formation was suggested by Bandyopadhyay (1988b) and Bandyopadhyay and Sengupta (1999, 2006). The other fossil-bearing Middle Triassic horizon of India, the Denwa Formation of the Satpura Basin, has not yielded any non-

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India	Rewa					Tiki									
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Zambia	Luangwa										.m∃	Itawere	N		
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Cosgriff (1984), Rubidge (1995), Bandyopadhyay Figure 8. Global correlation of the Triassic Gondwana horizons of India. Triassic time scale is after Ogg et al. (2016). Sources of information: and Sengupta (1999, 2006), Schoch et al. (2010), Ray (2015), Martz and Parker (2017), Datta et al. (2019b). mammalian cynodonts. Bandyopadhyay and Sengupta (1999) correlated it with the Holbrook Member of the Moenkopi Formation, U.S.A (Fig. 8). However, Abdala et al. (2005) directly correlated subzone C of the *Cynognathus* AZ of South Africa with the Denwa Formation based on the presence of *Paracyclotosaurus*, and considered the possible extension of the age to the latest Anisian based on the presence of two mastodonsaurids. Recently, a new capitosaurid temnospondyl, *Antarctosuchus*, a sister taxon to the Indian form *Paracyclotosaurus crookshanki*, has been described from the upper Fremouw Formation of Antarctica (Sidor et al., 2014). Based on this fossil fauna, the age of the Denwa Formation is considered as Anisian (Bandyopadhyay and Sengupta, 1999; Sengupta et al., 2016, 2017).

Late Triassic Global Correlation

The faunal records of Late Triassic horizons of the world are comparatively rich and complete. A variety of diapsids, including dinosaurs, emerged during this time and diversified throughout the world. Simultaneously temnospondyls and several amniotes faced extinction. A number of major tetrapod taxa such as metoposaurids, phytosaurs, aetosaurs, rauisuchids, poposaurids, trilophosaurs, diademodontids, traversodonts, chiniquodontids appeared in the Late Triassic, became the indigenous taxa of this time and disappeared by the end of the Triassic. Almost all the major group of extant terrestrial tetrapods, such as dinosaurs (including birds), pterosaurs, crocodylians, turtles, lepidosaurs, extant amphibians (frogs, salamanders and caecilians) evolved by the end of Triassic. The first mammaliaforms (Rowe, 1988) appeared during the Late Triassic. The appearance of dinosaurs and mammaliaforms near its close makes the Triassic a transitional period between the archaic tetrapods of the Palaeozoic, the rise and fall of the dinosaurs during the Mesozoic and the spectacular radiation of mammaliaforms during the Cenozoic.

In terms of climate the Late Triassic period had fairly moist and hot climate of monsoon type with an alternation of wet and dry seasons (Robinson, 1970; Preto et al., 2010). A significant episode of increased rainfall throughout the world took place during this time, especially at the boundary between the lower and upper Carnian (Preto et al., 2010). Subsequently, the late Carnian and Norian became climatically stable with some minor climatic changes. In Laurasia, a large number of Late Triassic faunas is known from the Chinle Formation of southwestern United States, Dockum Formation of Texas, Popo Agie Formation of Wyoming and Newark Group of eastern United States (Long and Murry, 1995; Heckert, 2004; Lucas, 2018), Keuper Group of Germany (Deutsche Stratigraphische Kommission, 2005; Gradstein et al., 2012), and Krasiejów and Lisowice of Poland (Dzik and Sulej, 2007; Dzik et al., 2008). Among the Gondwana continents the Late Triassic vertebrates are known from the Ischigualasto, Los Colorado and Cacheuta formations of Argentina (Bonaparte, 1978; Tucker and Benton, 1982; Rogers et al., 1993; Arcucci et al., 2004), Santa Maria and Caturrita formations of Brazil (Langer, 2007; Langer et al., 2018), Lower Elliot Formation of South Africa (Yates, 2003), Isalo II Beds of Madagascar (Flynn et al., 1999; Fortuny et al., 2019) and Argana Group of Morocco (Dutuit, 1972; Buffa et al., 2019).

In the current work, the post-Carnian age for the Chinle Formation in Arizona and New Mexico are considered based on radioisotopic data (Irmis et al., 2010, 2011; Olsen et al., 2011; Martz et al., 2013), where Otischalkian and Adamanian are early Lacian (early Early Norian) and late Lacian (late Early Norian), respectively (Martz and Parker, 2017). Moreover, the Carnian-Norian boundary falls at about 228 Ma, and the duration of the Norian stage was long and comprises c.20 Ma (Gradstein et al., 2012; Ogg et al., 2016). Proliferation of Hyperodapedon in the lower Maleri fauna (about 60% of the total diversity, Benton, 1983) shows that it belongs to the Hyperodapedon biochron (sensu Lucas and Heckert, 2002) and the Ischigualastian LVF (sensu Langer, 2005), and a Carnian age was suggested for the formation (Langer, 2005). The lower Ischigualasto Formation of Argentina where Hyperodapedon dominated has been dated at 231.4±0.3 Ma (Martínez et al., 2011), i.e., late Carnian (Gradstein et al., 2012; Schultz et al., 2016). Langer et al. (2017) hence suggested a late Carnian to earliest Norian age for the horizons where Hyperodapedon is abundant, including the lower Maleri Formation. Although the lower Maleri Formation has yielded aetosaurian remains (Bandyopadhyay, 2011) these are yet to be studied in details. On the other hand, the metoposaurid temnopondyls are not robust Late Triassic biomarkers (Martz and Parker, 2017) as these have a long range extending from middle/late Carnian to middle/late Norian. Moreover, their global distribution is genera-specific as Koskinonodon and Apachesaurus are known from Noth America, Metoposaurus is from Europe, Arganasaurus and Dutuitosaurus is from Morocco and Panthasaurus from India (Chakravorti and Sengupta, 2019; Bufa et al., 2019). However, presence of *Exaeretodon* (Chatterjee, 1982) suggests a Late Carnian age for the lower Maleri Formation as this genus is essentially known from the late Carnian Hyperodapedon AZ of Santa Maria Formation of Brazil (Langer et al., 2007), and the Ischigualasto Formation of Argentina (Abdala and Ribeiro, 2010). In addition, the lower Maleri Formation is correlated with the Isalo II Beds (Madagascar), the Lossiemouth Sandstone (England), and the Middle Keuper (Germany, Fig. 8).

It is to be noted that the Bhimaram Formation, underlying the Maleri Formation is poorly fossiliferous and has yielded fragmentary remains of temnospondyl amphibians and dicynodonts (Kutty et al., 1987). Bandyopadhyay and Sengupta (2006) assigned an age of Middle Triassic (late Anisian to Ladinian) to the formation. Hence, a distinct age gap is evident between the Bhimaram Formation and the overlying lower Maleri Formation.

The upper Maleri Formation has yielded a diverse assemblage, including different sauropodomorphs. This distinctly younger upper Maleri fauna may be correlated with the Lower Elliot Formation of South Africa, lower part of the upper Mackay Formation of Madagascar, and lower parts of the Rio Blanco and Los Colorados Formation, Argentina (Fig. 8). An early Norian age has been proposed for this upper Maleri fauna (Bandyopadhyay, 2011). Although an age gap was suggested between the lower and upper fauna of the Maleri Formation (Langer, 2005), later workers (Bandyopadhyay and Sengupta, 2006; Bandyopadhyay, 2011) did not support this view (Ray, 2015).

The fossil assemblage of the lower Dharmaram Formation is essentially an archosaur-dominated tetrapod fauna, which is distinctly different from that of the underlying upper Maleri Formation. The lower Dharmaram fauna resembles post-Ischigualastian assemblages, such as that of the La Esquina Fauna of the Los Colorados Formation, the Trossingen Formation of the German Keuper, the lower Elliot Formation and the Chinle Formation, and is probably latest Norian– Rhaetian in age (Bandyopadhyay and Sengupta, 2006; Kutty et al., 2007; Novas et al., 2011; Bandyopadhyay, 2016).

An association of Hyperodapedon, the derived phytosaurs

including Volcanosuchus and Panthasaurus is found in the Tiki Formation of the Rewa basin. Based on its palynofloral assemblage (Maheswari and Kumaran, 1979) and faunal content (Bhat, 2018 and references therein), the Tiki Formation has been correlated with the lower Maleri Formation of the P-G Basin (Lucas, 1998; Datta, 2004) and the Camp Springs Member of the Dockum Formation, U.S.A. (Datta et al., 2004). A Carnian age was suggested for the Tiki Formation (Datta, 2004; Mukherjee et al., 2012). It is evident that the Tiki fauna may be placed within the Hyperodapedon biochron (Lucas and Heckert, 2002) and the Ischigualastian LVF (Langer, 2005) based on the abundance of Hyperodapedon in the fauna (Mukherjee and Ray, 2012). Ray (2015) showed that the Tiki Formation may be correlated with other horizons such as the lower part of the Pebbly Arkose Formation, Zimbabwe, base of the Isalo II Beds (Mackay Formation) of Madagascar, upper part of the Alemoa Member of the Santa Maria Formation, Brazil, Wolfville Formation of Nova Scotia and Popo Agie Formation of Wyoming (Fig. 8). Recently, a rich assemblage of freshwater sharks, ceratodontiform dipnoans, xenacanthids, and actinopterygians, and varied archosauriform teeth has been reported, and shows similarity in faunal assemblage with that of the lower Tecovas Formation of the Chinle Group (Ray et al., 2016; Bhat et al., 2018a, b), which is early/middle Norian in age (Martz and Parker, 2017). Moreover, Datta et al. (2019a, b) reported the presence of more derived phytosaurs and absence of the basal Parasuchusi from the formation. Hence, a late Carnian to early/middle Norian age is proposed for the Tiki Formation.

Jurassic Vertebrate faunas

Faunal Characteristics

The end-Triassic witnessed an extinction event which is considered as one of largest of the five major extinction events (Benton, 1986; Olsen and Sues, 1986, Whiteside et al., 2010). At the onset of the Jurassic when the supercontinent Pangaea started to break up, world continued to be warm and arid in low- to mid- latitudes in western Pangaea as indicated by the high latitude floras in Siberia and lack of glacial deposits. While in the Late Jurassic this arid zone spread towards southern Eurasia (Hallam, 1984). Sea levels began to rise because of increase in sea-floor spreading and subsequently large areas of the continents were flooded, the deserts began to retreat, and continental temperatures stabilized (Tennant et al., 2016). The typical Dicroidium-Ptilophyllum flora of the Gondwana was replaced by a conifer-benettetilean flora of the Jurassic (Chatterjee et al., 2017). A short-lived but widespread marine transgression at the beginning of Jurassic resulted in advancement of shallow seas across the continents (Haq, 2017), as a result of which the Early Jurassic terrestrial fossil record is scarce (Tennant et al., 2016). India is no exception and the terrestrial tetrapods of the Jurassic period are found only from P-G Basin (Bandyopadhyay, 1999). There are two horizons, which have produced Early Jurassic vertebrates, and these included the Kota Formation and the underlying upper part of the Dharmaram Formation (Bandyopadhyay and Roychowdhury, 1996). The upper Dharmaram fauna includes two sauropodomorphs, Lamplughsaura dharmaramensis and Pradhania gracilis, a theropod similar to Dilophosaurus, and a sphenosuchid similar to Dibothrosuchus (Kutty et al., 2007).

The overlying Kota Formation has been subdivided into two lithological units (Rudra, 1982); the lower unit is dominated by

fluviatile sandstone-mudstone association while the upper part includes marl and limestone beds. Rudra and Maulik (1994) suggested that a meandering river system deposited the lower Kota and a braided river system formed the upper part. Interestingly two distinct biozones have been identified, where the lower fauna contains two sauropods, Barapasaurus tagorei (Fig. 9A) and Kotasaurus yamanpalliensis (Fig. 9B-C), an ankylosaur (Galton, 2019), a kuehneotheriid, an amphilestid, and a morganucodontid (Table 4). From the limestone of the upper part of the Kota Formation a diverse vertebrate fauna has been reported, which includes three semionotid genera, two pholidophorids, a coelacanthid, a kayentachelyid, a campylognathoidid, two sphenodontians, and a lepidosaur. In addition, there are seven mammaliaformes (Table 4) including two docodontids, a morganucodontid, and an amphilestid (Bandyopadhyay et al., 2010). The fauna also contains three mammaliaformes of uncertain affinities (Table 4).

Intercontinental relationships

Early Jurassic tetrapod assemblages are known from the McCoy Brook Formation of Nova Scotia, Canada (Sues et al., 1994; Fedak et al., 2015), Moenave, Kayenta and Navajo formations, Arizona, in USA (Schoch et al., 2010), La Boca Formation of Tamaulipas, Mexico (Clark et al., 1994), and Lufeng Formation of Yunnan, China (Lucas 2009). In the Gondwanan region, the Elliott and Clarens formations of South Africa (Knoll, 2005) and the Fallan Formation of Antarctica (Hammer and Hickerson, 1996) are known for their Early Jurassic vertebrates. The sedimentary succession of the Cañadón Asfalto continental basin in the Argentinean Chubut Province of central Patagonia preserves a rich record of Jurassic vertebrate fauna. A sauropod-dominated fauna occurs in the Las Leoneras Formation, which is Early Jurassic (Sinemurian to Pliensbachian) in age (Pol et al., 2011). The next stratigraphically higher fauna occurs in the Early-Middle Jurassic Cañadón Asfalto Formation (Cúneo et al., 2013). The Morrison Formation of USA (Foster, 2003) and the Tendaguru Beds of Tanzania (Remes, 2007) are well known for their Late Jurassic vertebrate fossils. However, most of the Early Jurassic vertebratebearing horizons of Europe are marine deposits (Delsate and Ezcurra, 2014).

In the light of studies on faunal turnover during Triassic-Jurassic boundary by Olsen and Galton (1977) and Benton (1986), the upper Dharmaram fauna represents the record of earliest Jurassic tetrapods and a Hettangian age was assigned to the formation (Bandyopadhyay and RoyChowdhury, 1996; Bandyopadhyay and Sengupta, 2006). The fauna consists of two basal sauropodomorphs, a sphenosuchian similar to Dibothrosuchus of the Lower Jurassic Lufeng Group, China and a large theropod similar to Dilophosaurus of the Lower Jurassic Kayenta Formation, Arizona (Kutty et al., 2007; Novas et al., 2011). These authors further stated that the upper Dharmaram fauna is similar to the faunas from the Upper Elliot and Clarens formations of South Africa, the Kayenta Formation of USA and the lower Lufeng Group of China, and suggested an Early Jurassic age (Sinemurian) for this horizon. On the other hand, the Kota Formation has long been considered to be of Liassic age (King, 1881; Robinson, 1970) on the basis of its varied fish assemblage. Analyzing the faunas of the lower and upper units of the Kota Formation and comparing them with faunas from coeval horizons, Bandyopadhyay and Roychowdhury (1996) and Bandyopadhyay and Sengupta (2006) assigned the lower Kota fauna to an age ranging from Sinemurian to Pliensbachian and



Figure 9. Sauropod dinosaurs of the Kota Formation, A-B, Barapasaurus tagorei, A, a mounted skeleton; B, mounted manus in anterior view; C-D, Kotasaurus yamanpalliensis, C, mounted neck and skull; D, a mounted skeleton.

Table 4	. Vertebrate	fossil assem	blage of the	Jurassic Ko	ta Formation	of
India (a	fter Bandyo	padhyay et al	l., 2010; Parn	nar et al., 201	3, Galton, 201	19)

Family/clade	LOWER FAUNA	UPPER FAUNA
PISCES		
Semionotid	-	Lepidotes deccanensis
	-	Paradapedium egertoni
	-	Tetragonolepis oldhami
Pholidophorid	-	Pholidophorus kingi
	-	P. indicus
Coelacanthid	-	Indocoelacanthus robustus
TESTUDINATA	-	
Kayentachelyidae	-	Indochelys spatulata
DIAPSIDA		
Campylognathoididae	-	Campylognathoides indicus
Sphenodontia	-	Rebbanasaurus jaini
	-	Godavarisaurus lateefi
Lepidosauria	-	Bharatagama rebbanensis
Sauropodomorpha	Barapasaurus tagorei	-
	Kotasaurus yamanpalliensis	-
Ornithischia	Ankylosauridae	-
MAMMALIA	-	-
Docodontidae	-	Gondtherium dattai
Morganucodontidae	Indotherium pranhitai (=Indozostrodon simpsoni)	Indotherium pranhitai
?Amphilestidae	Indotherium pranhitai	Paikasigudodon yadagiri
Incertae sedis	-	Dyskritodon indicus
Kuehneotheriidae	-	Kotatherium haldanei
Eobaataridae		Indobaatar zofiae
Incertae sedis	-	Nakunodon paikasiensis
Incertae sedis	-	Trishulotherium kotaensis

the upper Kota fauna to Toarcian, which may be extended to the Middle Jurassic (?Aalenian).

Discussion and Concluding Remarks

In the backdrop of a Pangaean landscape, certain macroevolutionary patterns and major transformations of vertebrate evolution, especially of the tetrapods, are evident in the highly diverse Gondwana fossil records of India. During the Late Permian, the dicynodont-dominated fauna of the Kundaram Formation closely resembles the dicynodont radiation in other Gondwanan regions, especially the Beaufort Group of the Karoo Supergroup, South Africa (Ray, 1999). The Permian-Triassic boundary in India is represented by the transition from the Kundaram to the Kamthi formations of P-G Basin and from the Raniganj to the Panchet formations of the Damodar Basin. The generic diversity of the dicynodonts decreased drastically at the onset of the Triassic (Fig. 10) as *Lystrosaurus* is the

only known genus from the Panchet and Kamthi formations. This steady decrease is also true for the synapsid (excluding the early mammals) diversity. Although collection bias cannot be ruled out, such decrease in taxic diversity is correlated with the end-Permian mass extinction, which resulted at least in part from a large scale destabilization of carbon cycle (Bond and Grasby, 2017).

After the end-Permian extinction event, most of the ecological niches became almost vacant, as a result of which the Early Triassic exhibited a low faunal diversity, with *Lystrosaurus*, accounting > 90% of the terrestrial vertebrates together with rare amphibians, but without diverse herbivores and top predators (Benton, 1983; Chen and Benton, 2012). However, Damiani et al. (2003) discovered a more diverse tetrapod assemblage from the Early Triassic Lystrosaurus AZ exposures in Barendskraal of South Africa. The capitosaurs and trematosaurids flourished during this period whereas the archosauriforms formed a minor component. A similar faunal transition is depicted by the Panchet fauna (Fig. 10), which shows a highly diverse temnospondyl radiation involving several families such as the trematosaurid, benthosuchid, rhytidosteid, lapillopsid, tupilakosaurid and brachyopid temnospondyls, which is comparable with that of other coeval Gondwanan and Laurasian regions. Mukherjee et al. (2010) suggested that the small size of the trematosaurids and Lystrosaurus (Shishkin et al., 1996; Ray, 2005) reflects the 'Lilliput effect' as documented by Twitchett (2007). Moreover, the fast growth strategy adopted by the trematosaurids was linked to the rapid invasion of various empty Panchet ecological niches in the aftermath of the end-Permian mass extinction (Mukherjee et al., 2010). The Panchet and Kamthi fauna may be considered as the late Palaeozoic 'holdover' fauna as described by Romer (1966) and Padian and Sues (2015).

A significant change occurred in the composition of terrestrial tetrapod communities during the Middle Triassic. The diversity and the number of archosauromorphs especially the rhynchosaurs increased considerably. Two principal lineages of Archosauria, Ornithodira and Crurotarsi and two groups of therapsids, kannemeyeriiform dicynodonts and gomphodont cynodonts, appeared and diversified considerably in the Gondwanan regions (Fraser and Sues, 2011). In India although a decrease in diversity at the temnospondyl family-level is evident during the Middle Triassic (Fig. 10), several new capitosaur taxa such as Paracyclotosaurus crookshanki and Cherninia denwai of the Denwa Formation appeared during this time. This period also witnessed the radiation of the dicynodonts, albeit in small numbers compared to the Late Permian diversity (Fig. 10) and is represented by several kannemeyeriiform taxa from the Yerrapalli and Denwa formations (Table 2). Moreover a decrease in dominance of the synapsids, and increase in diversity and radiation of the diapsids (archosauromorphs) in the form of rhynchosaurids, allokotosaurs, aphanosaurs and erythrosuchids (Fig. 10) is also noticed in this period.

During the Late Triassic, terrestrial ecosystems exhibited widespread and dramatic changes in the composition of vertebrate communities resulting in a biologically diverse fauna (Sues and Fraser, 2010; Irmis and Whiteside, 2011). Taxonomic richness was a rapidly ascending phenomenon whereas taxonomic relative abundances were qualitatively quite stable in the Late Triassic (Olsen et al., 2011). Morphological disparity was relatively high during this time (Brusatte et al., 2008) and evidence of high biogeographic provinciality was provided by Olsen et al., (2011) from the Norian–Rhaetian Chinle– Dockum assemblages and the Germanic basin type assemblages of





Figure 10. Graphical representation of the Permian-Jurassic taxic diversity in the different Gondwana stratigraphic horizons of India. Subsequently darker shades of grey indicate subdivision of the Triassic into Early, Middle and Late. Sources of information: Chatterjee (1980, 1982, 1987), Bandyopadhyay (1999, 2011), Ray (1999, 2001), Kutty et al. (2007), Novas et al. (2011), Kammerer et al. (2016), Mukherjee and Ray (2014), Chakravorti and Sengupta (2019), Ray et al. (2016, 2019).

the Central Europe and Greenland of Carnian-Rhaetian age. Both the 'archaic' and the 'modern' taxa are noted during the Late Triassic. The dicynodont therapsids, procolophonid parareptiles and chroniosuchian anthracosaurs represented the 'archaic'. The ancestors of modern tetrapod communities such as the crocodyliforms, lepidosaurs, mammaliaforms and turtles appeared during Late Triassic, along with the oldest frogs, salamanders and caecilians, dinosaurs, pterosaurs and mammals, which also had their origin during this period (Fraser and Sues, 2011). Similar high diversity and radiation of vertebrates are also seen in the Indian scenario, especially in the advent of different types of freshwater fishes (hybodontids, xenacanthids, actinopterygians and dipnoans), temnospondyls (metoposaurids and chigutisaurids) archosauromorphs (archosauriforms, phytosaurs and basal saurischians including sauropodomorphs), and cynodonts including the early mammaliaforms. This period is characterized by the appearances and disappearances of 'indigenous fauna' such as the phytosaurs and appearance of 'living' fauna (sensu Romer, 1966; Padian and Sues, 2015), which included the basal saurischians and mammaliaforms. The Late Triassic vertebrates of India comprise distinct faunal assemblages, which are more or less comparable to the global Triassic vertebrate faunachrons, especially of the Carnian (sensu Lucas, 1998, 2010; Gradstein et al., 2012; Tanner, 2018). The Triassic-Jurassic transition is marked by a distinct faunal change, where the phytosaurs and aetosaurs of the upper Maleri and lower Dharmaram changes to a new upper Dharmaram fauna comprising sphenosuchians (Bandyopadhyay and Sengupta, 2006). This marked biotic turnover may be correlated with the drastic climatic change at the Triassic-Jurassic transition, which experienced global warming because of a four-fold increase in atmospheric CO₂ that probably derived from volcanism (Bond and Grasby, 2017; Tennant et al., 2017).

Hence, it may be concluded that the Late Permian-early Middle Jurassic Gondwanan vertebrates of India reflect major global faunal fluctuations and transitions, macroevolutionary patterns and constitute important biostratigraphic markers for global correlation of the Indian stratigraphic horizons.

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