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TETRAPOD FAUNAS FROM SOUTH AMERICA AND INDIA: A PALAEOBIOGEOGRAPHIC INTERPRETATION

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The faunal relationships of the continental tetrapods of India and South America are the result of the presence of the "Gondwanian Cretaceous Fauna" on most of the Gondwanian continents, and whose identity persisted until the Late Cretaceous. With that objective, the Late Cretaceous families from India are briefly reviewed. Six families of Gondwanian tetrapods are recognized in India: Boidae, Pelomedusidae, Abelisauridae, Titanosauridae, Nodosauridae and Sudamericidae, along with three families of Laurasian origin: Pelobatidae, Discoglossidae, and Palaeoryctidae. The resulting analysis suggests that 66% of the Cretaceous families of Late Cretaceous tetrapods from India are present in South America.

It is recognized that the marine barrier between Madagascar-India and mainland Africa probably did not prevent the faunal flux between such landmasses. The supposed affinities of the Morrison and Tendaguru dinosaurs faunas are discussed. It is concluded that the Late Jurassic fauna of Tendaguru would represent the first sample of the Gondwanian fauna, resulting from the palaeobiogeographical isolation between Laurasia and Gondwana, possibly established in the Early Jurassic.

Key Words: Tetrapods Faunas; Late Cretacious; Titanosaurid Dinosaurs; Cretaceous Tetrapods; Palaeogeographic Reconstructions

Introduction

The titanosaurid dinosaurs, and the genus *Titanosaurus* in particular, recorded from the Upper Cretaceous of India [1,2] and South America [3,4] have stimulated speculations on the faunal relationships between these two subcontinents during the Upper Cretaceous [2,4]. The evidences of the inferred faunal relationships have only increased after the cited papers. Though not abundant, they are significant, because besides Titanosaurus, several groups of tetrapods common to both subcontinents have been recorded. They are the theropods *Indosuchus* and *Indosaurus*[2] recognized as part of the South American family Abelisauridae[5,6]; the pelomedusoid turtles[7] well recorded in the Upper Cretaceous of South America[8]; the booid snakes[9,10,11] and personal observations; ankylosaur dinosaurs[12,13]; and multituberculates mammals of the Family Sudamericidae[14] originally recorded in the Upper Cretaceous[15] and Early Palaeocene of South America.

The evidences from the Late Cretaceous tetrapod record of India and South America suggesting faunal relationships have not been widely confirmed by geophysical, palaeomagnetic and geological studies, which on the contrary suggest a long period of isolation for India before its collision with Asia. However, a physical connection between Antarctica and India in the Late Cretaceous, until 80 my ago has been postulated[14,16].

For complicated palaeogeographic situations, as in the case for India, the palaeontological information based on continental tetrapods has been demonstrated to be useful. The case for faunal interchange between North and South America during the Late Cretaceous, is mostly documented through the presence of titanosaurids in southwestern North America[17,18] and *of Kritosaurus-like* hadrosaurs in southern South America[5,19]. The interchange probably occurred during the Campanian between southern Central America and northwestern Colombia[20,21], even though geophysical data is not supportive of this[22]. Notwithstanding, all the faunal relationships suggested by the fossil record cannot be explained in a similar way.

The hypothesis of the existence of a "Gondwanian Cretaceous Fauna"[5] seems to be consistent with the global record of tetrapods[23]. Such a fauna was characterized by leptodactylid

and pipoid anurans, by chelyd and pelomedusid turtles, by dinilysid and booid snakes, by the notosuchians, peirosaurid and sphagesaurid crocodiles, by the pterodaustrid pterosaurs, by abelisaurid, cacharadontosaurid and alvarezsaurid theropods, by the dicraeosaurid, rebbachisaurid and titanosaurian sauropods, and by the gondwanatheres and dryolestoid mammals. This "Gondwanian Cretaceous Fauna" shows outstanding compositional differences with the "Laurasian Cretaceous Fauna" [5,23] an interpretation which is not denied by recent discoveries in Africa and Madagascar[14,24,25,26,27,28]; in India[14] and South America[25,29,30,31].

In this article some information and comparisons to the Cretaceous tetrapod assemblages of India and South America is given. It is emphasized that the faunal relationships do not necessarily imply the existence of direct physical connections; they may also be the result of a widespread continuous fauna before the fragmentation of the Gondwana supercontinent.

Cretaceous Tetrapods of South America

The record of continental Cretaceous tetrapods of South America was discussed by Bonaparte[78] and partially by Novas[25] only on the basis of dinosaur distribution. The list of families recorded in South America and their presence in Africa, Madagascar and India (Table I) shows the taxonomic diversity which, not without limitations, provides some information for palaeobiogeographic discussions. In the Cretaceous families included are *Unenlagidae nov.* comprising the South American genus *Unenlagia* and the *Malgache* genus[27]. The close similarities in the morphology of the scapulae, ischia, and pubic of both genera suggest they are members of the same family. The rather rich Cretaceous fauna of South America is significant enough for any discussion on the evolution and palaeobiogeography of the Gondwanian Cretaceous tetrapods. Obviously, its taxonomic diversity in larger than that from any other landmass of the southern Hemisphere.

While at the generic level most of the listed taxa are known only from South America, except questionably perhaps for *Laplatasaurus, Titanosaurus, Antarctosaurus, Araripesuchus,* at the family level the identity with India is very significant because of the 9 families recorded from that subcontinent 6 of them (66%) are present in South America.

The difference in the number of Cretaceous families recorded in South America (45) and India (9) possibly does not reflect the real situation. It may be only the result of sampling intensity and sedimentological differences in one and another region. The cited differences may be substantially reduced in the near future. Albeit despite the significant disparity of information from both regions, the study and discussion on their Cretaceous tetrapods may be helpful to define some conceptual aspects on the subject.

Cretaceous Tetrapods of India

The few families of Cretaceous tetrapods known from India probably are only a small sample of the taxonomic diversity present in that subcontinent. Several taxa are fragmentarily represented as *Compsosuchus solus, Laevisuchus indicus, Jabbulpuria tenuis, Coeluroides largus, Dryptosauroides largus, D?. grandis, Ornithomimoides mobilis,* and *0 Barasimlensis.* These taxa are of uncertain taxonomic interpretation[2]. However, the material on which these are based appears to be adequate enough to demonstrate that the diversity was larger than that shown from the families indicated in Table I.

In this paper the families Compsognathidae, Coeluridae and Omithomimidae recognized[2], are not included because of the meager anatomical-comparative basis on which they were recognized. The specimens studied by these authors are poorly preserved but in the context of South American tetrapods, we could possibly refer some of them, with better comparative basis, to Noasauridae or to the Alvarezsauridae. At the same time some of these specimens may represent endemic families of India or Gondwana, or eventually may be Laurasian immigrants as in the case of Palaeoryctidae[32] and Pelobatidae[33]. It is more reasonable not to include the above cited families for palaeobiogeographic analysis and interpretations.

The case is different for the genera *Indosaurus* and *Indosuchus* which although fragmentarily represented[13], the material on which are based have been discussed[5,6,13,25,34,35]. At present there is consensus to consider both genera as Abelisauridae, without close relationships with Allosauridae or Tyrannosauridae[2, 35].

The presence of the Late Cretaceous families Pelobatidae[33], Discoglossidae[36], and Palaeoryctidae[10,32] have been interpreted by the cited authors as immigrants from Asia which is agreeable.

In general terms, the record and information on Cretaceous tetrapods from India was not significantly increased after Huene and Matley monograph, except for the Pelomedusidae[7,37]; for a theropod[38]; for a titanosaur braincase; for the record of Pelobatidae[33]; with some doubts on discoglossid anurans[36]; for a titanosaurid[40]; for a palaeoryctid mammal[32]; and for *Indosuchus* skeleton and titanosaurian braincases[13]. The author considers that the record of the Cretaceous tetrapods from India shall be greatly increased in the near future through methodical and continuous field work.

Meanwhile, the available evidence demonstrates an outstanding familiar identity with the South American and African tetrapods. It is clear that this situation has an important palaeobiogeographic implication which we will attempt to interpret.

Palaeogeography

The palaeogeography of Gondwana during the Cretaceous is a subject to which many scientists around the world are seriously contributing. However, the basic information presented here is still accurate enough to serve for palaeobiogeographical discussions, based on the available palaeontological information of continental vertebrates.

Isolation of Gondwana

After the union of the Tethys Sea with the Pacific Gondwana became a supercontinent isolated from Laurasia. The age of this outstandingly important palaeogeographic event is not precisely documented; it happened in Early Jurassic (Toarcian)[41,42]. If such an isolation actually took place at that time, it may represent a more significant biogeographical event, not only for the evolutionary history of the Mesozoic tetrapods but for the whole Mesozoic continental life.

The Early and Middle Jurassic was a critical time for the evolution of several tetrapod groups of archosaurs and mammals. Both groups were in a rather primitive level of organization but with a rich potential of diversification and improvement of their anatomical organization as it is demonstrated by the Late Jurassic and Cretaceous record both from Laurasia and Gondwana. So, the inferred isolation of the Early Jurassic Pangaean tetrapods in two extensive biogeographical regions may have triggered a continuous and gradual differentiation of the Gondwanian and Laurasian communities of tetrapods[5].

Fragmentation of Gondwana

In general terms the magnetic anomaly data derived from the seafloor record documents the break-up of the geometry of the Gondwana continents from the Middle Jurassic onwards, from about 180 my ago. More in detail, the separation of Madagascar-India-Antarctica-Australia from main land Africa-South America is possibly the first documented step in the fragmentation of Gondwana, with a estimated age of 160 my ago[43-45]. Later, around the 135 my ago, India began to move away from Madagascar, but possibly remained linked to Antarctica until 80 my ago[14].

Isolation of India would have began after its separation from Antarctica around the Coniacian, 80 my ago[16,26], and appears to have ended in Maastrichtian times as Asian pelobatids[33], and Palaeoryctidae mammals[32] are recorded in the Lameta and Intertrappean Beds. In addition, possible discoglossids[36], and Alligatorinae crocodiles have been cited from these beds. Some microfossil of Laurasian affinities are also recorded in the same beds: ostracods[46, 47], charophytes[10], as well as palynofloral assemblage[48].

It is generally agreed that the opening of the south Atlantic began from the South in the Late Jurassic-Early Cretaceous[22], but the complete opening of the South Atlantic, connecting it with the Tethys was only in the Late Cretaceous[43].

Antarctica remained connected to South America through the Antarctic Peninsula until the Oligocene[26], and with India eventually until the Coniacian through the Kerguelen Plateau[14]. Australia became isolated from Antarctica in the Late Cretaceous[43], but the presence of a lower Palaeocene Omithorhynchidae in southern south America suggests the isolation may have been later[49].

The early separation of Madagascar-India from mainland Africa is not clearly supported by the palaeofaunal evidence. Similarly the eventual isolation of Madagascar, since 135 my ago[50] is not supported by the Late Cretaceous faunal evidence from Madagascar[26,51,52,53]. If Madagascar was

Table I

Families recorded in South America and their presence in Africa, Madagascar and India showing taxonomic diversity

South America	Africa	Madagascar	India	Australia
Pipidae	x			
Leptodactylidae				
Chelydae				
Pelomedusidae	x		x	
Araripemydidae	x			
Iguanidae				
Dinilysidae				
Boidae			x	
Baurusuchidae				
Sphagesauridae				
Notosuchidae	x			
Araripesuchidae	x	x		
Dolichochampsidae				
Pterodaustridae				
Anhangueridae				
Cearadactylidae				
Tapejaridae				
Criorhynchidae				
Dsungaripteridae				
Nyctosauridae				
Stegosauridae				
Dryosauridae				
Hadrosauridae				
Nodosauridae			x	
$_6$Ceratopsidae				
Abelisauridae	X?	x	x	
Noasauridae				
Velocisauridae				
Alvarezsauridae				
Unenlagiidae nov.		x		
Carcharodontosauridae	x			
Titanosauridae	x	x	x	
Andesauridae				
Patagopterydae				
Enantiornithidae				
Avisauridae				
Ferugliotheridae				
Sudamericidae		x	x	
Austrotriconodontidae				
Bondesiidae				
Dryolestidae				
Mesungulatidae				
Reigitheridae				
Brandoniidae				
Barbereniidae				

separated from mainland Africa by a marine barrier, probably it did not prevent some degree of tetrapod interchange between both landmasses, as is the case for the Cenozoic history of Madagascar[14].

Based on palaeogeographic reconstructions[14,16] inferred faunal connections between Antarctica and India-Madagascar through the Kerguelen Plateau until 80 my ago. The hypothesis is interesting and though based on recent information, is still open to great uncertainty. The faunal identity between Late Cretaceous tetrapods of Madagascar and South America implies a closer palaeobiogeographic relationship.

The Common Families Recorded in South America and India

The faunal list of South American and Indian Late Cretaceous tetrapods shows that of the nine families recorded in India, six of them are present in South America, and the remaining three (e.g. Pelobatidae, Discoglossidae and Palaeoryctidae) in Asia. All the available evidence suggest that the Asian families colonized India when this subcontinent was in contact with Asia, through island dispersals, which permitted the colonization of terrestrial tetrapods, even before the major physical collision.

The six families recorded in both India and South America have an important palaeobiogeographic implication, and the basis for identification of such families are discussed here according to the available evidence from each region.

Pelomedusidae

On *Shweboemys pisdurensis* from the Maastrichtian of Central India, represented by a nearly complete skull, and ten specimens with almost complete skeleton, referred to this species are known[7]. A detailed review of the knowledge on the Pelomedusidae from India, accompanied a careful description of the plastron and comparisons of skull morphology of the four species *of Shweboemys*[7]. The knowledge of this Late Cretaceous pelomedusid from India is good and its identification as Pelomedusidae appears to be firm.

Pelomedusids from the Late Cretaceous of South America were described and recorded in different localities of Brazil and Argentina[54-56].

Boidae

Evidences of snakes have been frequently cited from the Late Cretaceous of India[9]. Reference to Madtsoinae was made[10] but, it is known that there is no specific publication on the subject.

Boidae gen et sp indet is known from the Intertrappean Beds of Kachchh[11]. A study was conducted in the palaeontological collection section of the Geological Studies Unit, Indian Statistical Institute, Calcutta, by the author with kind courtesy of Professor S L Jain to investigate a block of matrix from the Intertrappean Beds with natural molds of an articulated sequence of vertebrae, which was tentatively interpreted as of *Booidea indet.*, (pers obs). The evidence for the presence of Boidae in the Late Cretaceous of India is not definitively proved, but the available information is significant to indicate the presence of such group of snakes.

From the Late Cretaceous of South America, Madtsoinae *Alamitophis; Patagoniophis,* and the probable Madtsoinae *Rionegrophis,* all of them based on complete vertebrae from the Campanian Los Alamitos Formation, are known [57-59].

Abelisauridae

Indosuchus raptorius and *Indosaurus matleyi* are represented by fragmentary skull material which were originally assigned, not without doubts, to the Allosauridae (Huene and Matley[2]). Later, Chatterjee[35] considered both genera as Tyrannosauridae and Allosauridae respectively. Bonaparte[5] considered *Indosuchus* as a probable abelisaurid, and later[6] interpreted *Indosaurus* also as a probable abelisaurid based on the diagnostic characters of the maxilla.

More recently, Chatterjee and Rudra[13] reported the discovery of new postcranial material of *Indosuchus,* interpreted by them as an abelisaurid, and presented a reconstruction of the postcranium and of the skull. Although all this new evidences should be critically reviewed, it is clear that the presence of Abelisauridae in the Late Cretaceous of India is well documented.

From South America it was described the almost complete skull *of Abelisaurus comahuensis* was described by Bonaparte & Novas[60] along with the almost complete skeleton, and skull and jaws *of Carnotaurus sastrei* (Bonaparte[61]; Bonaparte *et al.*[62]). In addition, Martinez *et al.*[63] described some vertebrae and the hind limb bones *of Xenotarsos aurus bonapartei.* All the known taxa

of Abelisauridae from South America are from the Late Cretaceous, except *Ligabuemo andesi* which is from the Neocomian, and possibly more related to the Noasauridae than to the Abelisauridae.

Nodosauridae

Matley[12] described a sacrum, ilium, tibia and parts of the dermal armour of an ornithischian dinosaur, *Lametasaurus indicus,* interpreted as a stegosaurian from the Late Cretaceous beds which yielded *Indosaurus* and *Indosuchus.* Later, Huene and Matley[2], recorded some new material of the same taxon, such as scutes and some evidences that *Lametasaurus* had a club at the distal end of the tail. *Lametasaurus indicus* was originally interpreted as an armoured ornithischian dinosaur. However, Coombs and Maryanska[64] considered it as *nomina dubia;* and Molnar[65] pointed out that the material described by Matley[12] corresponds to a mixed-up collection of bones from an armoured form, possibly a sauropod, a crocodile and a theropod. Finally, Chatterjee and Rudra[13] considered *Lametasaurus* as an ankylosaur and reported additional diagnostic material as vertebrae, scapulo-coracoid, humerus, femur, and pieces of the dermal armour. No familiar relationships were indicated

Dravidosaurus blanfordi from Cretaceous marine beds, was originally considered as a stegosaurian by Yadagiri and Ayyasami[66]. However, according to Chatterjee and Rudra[13], the bones may correspond to those of marine reptiles.

From South America the evidence of Ankylosauria is limited, but it is based on a complete and diagnostic femur from the Late Cretaceous of northern Patagonia, suggesting Nodosauridae affinities[67].

Titanosauridae

Lydekker[1] coined the term *Titanosaurus indicus* for two caudal vertebrae from the Late Cretaceous of Bara Simla, Jabalpur. A second species, *T blanfordi* from the Late Cretaceous of Pisdura was also based on two caudal vertebrae.

Huene & Matley[2] listed the following titanosaurid genera for the Late Cretaceous of India: *Titanosaurus, Antarctosaurus, Laplatasaurus* and a genus indet. However, in a recent and detailed paper by Jain & Bandyopadhyay[40], a revision is made on the probable validity of these genera based upon the interpretations of McIntosh[69], Weishampel[69], Jacobs *et al.*[70], and their own observations. They conclude that the only valid genus is *Titanosaurus,* with four species: *T indicus, T blanfordi, T madagascariensis,* and *T colberti.* The description, figures and discussion of the titanosaurid *T colberti* given by Jain and Bandyopadhyay[40] demonstrate the undoubted presence of a typical titanosaurid with affinities to *Neuquensaurus ("Titanosaurus") Saltasaurus* from Argentina[71,72]. In accordance with the morphology of the scapula of *T colberti,* which is associated with a rather slender humerus, and the scapula and humerus of *"Antarctosaurus septentrionalis"* (Huene and Matley[2]; Swinton[73]), it is probable that more than one genus of titanosaurids was present in India.

In South America the record of Titanosauridae *sensu stricto* (Bonaparte[78]), with procoelian caudals all along the tail, have been recorded from the Coniacian Rio Colorado Formation through the Campanian-Maastrichtian Allem Formation of Patagonia, Argentina, and the Maastrichtian Lecho Formation of northern Argentina (Huene[4]; Bonaparte and Powell[72]; Powell[71,74]; Salgado & Coria[75]).

Sudamencidae

Recently, Krause *et al.*[14] communicated the discovery of a fragmentary postcanine from the Intertrappean sequence of Andhra Pradesh, India. The Sudamericidae (Scillato-Yane' & Pascual[76]) is a very derived family of multituberculate mammals "Gondwanatheria" (Mones[77]), interpreted by Kielan-Jaworowska and Bonaparte[79] as a suborder of the group. The Sudamericidae are made up of the South American genera *Sudamerica* and *Gondwanatherium* from the Late Cretaceous of Patagonia, characterized by hypsodont postcanines with a peculiar distribution of enamel on the occlusal surface.

The identification of the incomplete molar from the Late Cretaceous of India as a sudamericid is, probably, a correct interpretation because of the unusual distribution of the enamel, and the hypsodont condition of the tooth (Krause *et al.*[14]).

Of the six families of tetrapods common to India and South America, all of them except Ankylosauridae probably have a long evolutionary history in Gondwana. The record of the Ankylosauridae is restricted to the Cretaceous of the Laurasian continents, and if actually present in

India it may represent an Asian immigrants. If *Lametasaurus* is a Nodosauridae then it may be of Gondwanic origin as in the case[65] of the Australian genus *Minmi*. At present unfortunately it has been not demonstrated if *Lametasaurus* corresponds to one or the other family of the Ankylosauria.

Faunal Relationships Between South America and India

The similarities of the Late Cretaceous tetrapod faunas of South America and India do not mean that both subcontinents were in physical connection, but that the geographical distribution of such fauna involved in the intervening landmasses as well as in Africa and Madagascar, and eventually Antarctica and Australia. It seems clear that a basically homogeneous assemblage of tetrapods was present on most of the Gondwanan continents during the Cretaceous.

If the hypothesis of Schmidt-Efflng[41] and Hallam[42] that the Tethys Sea connected with the Pacific Ocean in the Early Jurassic is true, then it is clear that the early Mesozoic Pangaean fauna became biogeographically split into two, (e.g., one in Laurasia and the other remaining in Gondwana), well before the Cretaceous. The interpretation that such a palaeogeographical event is responsible for the different characteristics of the Late Jurassic and Cretaceous tetrapod assemblages of both Laurasia and Gondwana (Bonaparte[5]) appears to be confirmed by most of the numerous discoveries of Cretaceous tetrapods made on Gondwanan continents.

A review of the wellknown Late Jurassic faunas from Morrison and Tendaguru, may help to interpret that the faunal differences were already established before the Cretaceous. Here it is important to point out that the alleged similarities of the Late Jurassic Morrison and Tendaguru faunas (Galton[106]) it is not the result of detailed comparisons of the several taxa from each assemblage. The following objections appear to be valid against the supposed identity of the cited faunas:

1. The common presence of the genus *Dryosaurus* in the Morrison and Tendaguru beds proposed by Galton[106] is open to a different interpretation when the skulls of *Dtyosaurus altus* and *Dryosaurus lettow-vorbecki* illustrated by Galton[106] are carefully compared. The differences are seen in the morphology of the postorbitals, squamosals, jugals, parietals, supratemporal openings, etc. *Dysalotosaurus* studied in detail by Janensch[80] is a valid genus because of the so numerous differences in the skull structure with *Dryosaurus*.
2. The genus *Brachiosaurus* recorded in the Morrison and Tendaguru (Janensch[81] merits a comparative study of the presacral vertebrae because notable differences in structure of the neural arch are present in the American *B altithorax* and the African *B brancai*. Differences between the Morrison and Tendaguru species were reported by Paul[82], who proposed a different subgenus for the African species.
3. The genus *Barosaurus* recognized in the Tendaguru beds must be confirmed by comparative studies of the vertebral anatomy. McIntosh[83] has enunciated some doubts about its generic identification.
4. *Camarasaurus, Diplodocus, Apatosaurus, Haplocanthosaurus* and *Stegosaurus,* are not recorded in the Tendaguru assemblage, while *Dicraeosaurus, Janenschia, Elaphrosaurus* and *Kentrurosaurus* are not in the Morrison assemblage.
5. The theropod *Elaphrosaurus* is well documented only from the Tendaguru Beds. It exhibits pelvis and hind limbs characters of the gondwanan abelisaurid type.
6. The scarse osseous material from Tendaguru to the Morrison genus *Allosaurus* require restudy because there are significant differences in the proximal section of the femur (pers. observation).

It is concluded that the similarities of the Morrison and Tendaguru faunas are mainly ecological but not taxonomical. Both faunas may be the result of separate evolution from Pangean, Early Jurassic ancestors. The split in two large biogeographic regions of the Pangean tetrapods does not mean that after a few million years each endemic fauna would exhibit distinctive characters. More probably it was necessary a longer span of time until differential osseous characters evolved in each of the component taxa of the two isolated faunas, and so well manifested as to be realized by the palaeontologists, normally engaged with fragmentary material. Perhaps the Tendaguni fauna

is the oldest assemblage of the Gondwanan fauna, characterized by the sauropods *Dicraeosaurus, Janenschia* and *Tendaguria* Bonaparte *et al.* (in press), the theropod *Elaphrosaurus,* and the stegosaur *Kentrurosaurus.*

In the Cretaceous the endemic taxa appear to be widespread in different regions of Gondwana as it is explained below. The few available evidences from the Early Cretaceous (Neocomian) assemblage of La Amarga, Patagonia, Argentina, and the record from Wadi Ramon, Israel (Nevo[84]), give interesting information. From the former, the dicraeosaurid sauropod[85], the abelisaurid theropod[78] *Ligabuemo*, an unidentified stegosaur of the *Kentrurosaurus* type, and the pre-tribosphenic mammal[5] *Vincelestes* are known. From the latter assemblage of northeastern Africa pipoid frogs have been recorded (Nevo[84,86]; Baez[87]). In both cases bearing Gondwanan taxa.

Different palaeogeographic reconstructions of Gondwana for the Neocomian show that all its continents were physically connected, implying the possibility that the Early Cretaceous "Gondwanan fauna" was distributed on most of them.

For the Aptian-Albian the evidences of tetrapods are still scarce, although they are more numerous than for the Neocomian. The Araripe Basin of Northeastern Brazil yielded a variety of fishes and tetrapods of a marine coastal environment, as numerous pterosaurs (Kellner[88]), the crocodilian *Araripesuchus* also recorded in Africa (Buffetaut and Taquet[89]), the enigmatic theropod *Irritatosaurus* (Martill *et al.*[90]), the chelonian[91] *Araripemys*, and an undescribed small theropod (pers. observ.) possibly related to *Velocisaurus* from the Late Cretaceous of Patagonia[6].

The few records of continental tetrapods from the Araripe Basin are components of the "Gondwanan fauna". The pterosaurs, most of them endemic from South America, and the theropod *Irritatosaurus* are not palaeobiogeographically evaluated here.

The Aptian Anoual fossil locality of Marocco (Sigogneau-Russell *et al.*[92]) yielded a variety of amphibians (anurans, salamander-like, and possibly coecilians), turtles of the *Araripemys* type, sphenodontians, squamates, archosaurs, and mammals. Only the mammals from the Anoual assemblage (12 taxa) have been adequately studied (Sigogneau-Russell,[93-97]). Sigogneau-Russell *et al.*[92] recognized that *"Most of these taxa seem, sofar, to be endemic to Africa"*, except a symmetrodont, a triconodont amphilestid, and an indeterminated talonid of a tribosphenic mammal.

The Gadoufaoua fauna of the Aptian of Niger yielded several tetrapod taxa from the upper section of the Elrhaz Fm. and from the lowermost levels of the Echkar Fm. They were listed by as follow:

Chelonia - Pelomedusidae
Crocodilia - Pholidosauridae
Theropoda - Spinosauridae
Coelurosauria – Coeluridae
Sauropoda - Titanosauridae
Ornithischia – Iguanodontidae

Except for the Pholidosauridae and Iguanodontidae, the remaining taxa correspond to families recorded only or more frequently in Gondwana. The family Coeluridae is probably equivocal in referring to it the genus *Elaphrosaurus,* because it is probably a Ceratosaurian related to the abelisaurids (Holtz[98]). The Iguanodontidae is a family of world wide distribution, and have been recorded in Gondwana in the Cretaceous of Australia.

The Lightning Ridge fossil locality of Australia, considered as Aptian (Rich and Rich[99], Rich[100]) yielded several isolated tetrapod remains tentatively referred to the Laurasian families Hypsilophodontidae and Allosauridae. However, such interpretations require to be reconsidered after comparisons made with the new material of a basal iguanodontian from South America (Coria and Salgado[101], and with the new evidence of theropods from Africa and South America. The Early Cretaceous mammal from Southeastern Australia discovered and considered a possible placental by Rich *et al.*[102] suggests its endemicity to Australia.

Finally, the Aptian locality of Cerro Lc6n in northern Patagonia Formation Lohan Cura (Leanza and Hugo[103]) yielded *Agustinia ligabuei*[30] , an armoured titanosaur sauropod with three types of osteoderms articulating on the top of the neural spines of the vertebral column.

Jacobs *et al.*[104] communicated the discovery of an Early Cretaceous assemblage in Malawi, Africa, with titanosaurid dinosaurs and notosuchian crocodiles. The evolutionary degree of the titanosaurid *Malawisaurus* and the presence of the notosuchian *Malawisuchus* suggest close affinities

with taxa of Late Cretaceous age from South America.

What is available from the Aptian-Albian, and useflil for palaeobiogeographical discussion, strongly suggest well defined endemic characters for anurans, chelonians, crocodiles. sauropods, theropods and mammals, in most cases at the family level, and recorded in different Gondwanan continents. The evidence supporting this interpretation is far from numerous. However, it is significant enough as to assume that the "Cretaceous Gondwanan fauna" was distributed on all the continents of Gondwana before its fragmentation, which then produced isolated landmasses.

Conclusions

The affinities of the Indian and South American Late Cretaceous tetrapod faunas and the fossil record from Neocomian, Aptian-Albian and Late Cretaceous of Gondwana, suggest that a basically homogeneous faunal assemblage was present on large region of Gondwana during most of the Cretaceous. Another interpretation that the complete faunal isolation of India from Africa, Madagascar and South America would have begun so near the Late Cretaceous that the assemblage of tetrapods did not have enough time to substantially differentiate from one another. If we have in mind that the continental assemblage of tetrapods of Gondwana were relatively uniform until the Aptian-Albian and probably Cenomanian, it is probable that for the end of the Cretaceous such assemblages showed few changes, even when Gondwana was biogeographically fragmented. One explanation for the morphological conservatism may be that afier a prolonged period without immigratory events, the Cretaceous fauna of Gondwana would have reached an ecological equilibrium, with the varied ecological niches occupied by respective lineages during a long span of time, and without barriers for a free genetic interchange until the early Late Cretaceous.

The evolutionary trends which characterized the different groups of tetrapods possibly were defined during the Jurassic and maintained or eventually partly modified during the Aptian-Albian. They possibly continued until the Late Cretaceous on all the Gondwanan continents, even when the fragmentation of the supercontinent resulted in isolated communities of tetrapods.

The Late Cretaceous faunal interchange recorded between South and North America during the Campanian, (Rage[105]; Bonaparte[19]) and between Asia and India in the Maastrichtian, modified significantly the composition and characteristics of the old tetrapod assemblages of the "Gondwanian Cretaceous Fauna".

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