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The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction

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Abstract

The southern half of the main Karoo Basin in South Africa contains an almost continuous stratigraphic record of terrestrial sedimentation through the Permo-Triassic boundary (PTB). Detailed logging of multiple sections through the boundary sequence has defined the end-Permian mass extinction event using vertebrate fossils as well as a synchronous change in fluvial style reflecting a rapid aridification of climate. Field data demonstrates a 69% mass extinction of Late Permian terrestrial vertebrates lasting some 300 kyr terminating at the PTB, followed by a lesser extinction event (31%) approximately 160 kyr later involving four survivor taxa that crossed the PTB. The Early Triassic recovery fauna comprises proterosuchian archosauromorphs (*Proterosuchus*), small amphibians (*Micropholis, Lydekkerina*), small procolophonoids (*'Owenetta' kitchingorum, Procolophon*), medium-sized dicynodonts (*Lystrosaurus*) and small insectivorous cynodonts (*Progalesaurus, Galesaurus, Thrinaxodon*). Taphonomic bias towards preferential preservation of drought accumulations in the Early Triassic has probably over-emphasized the abundance and diversity of semi aquatic and burrowing animals. ***To cite this article: R. Smith, J. Botha, C. R. Palevol 4 (2005)***.

Résumé

La restauration de la diversité des Vertébrés terrestres dans le bassin du Karoo d'Afrique du Sud, après la crise biologique de la fin du Permien. Un enregistrement stratigraphique presque continu de la sédimentation terrestre du passage Permien–Trias (PTB), se trouve exposé dans la moitié méridionale du principal bassin du Karoo, en Afrique du Sud. Des relevés lithologiques détaillés de nombreux affleurements, englobant la séquence PTB, ont permis de définir l'événement des extinctions en masse de la fin du Permien à partir des vertébrés fossiles ainsi qu'à travers un changement contemporain du régime fluviatile, traduisant une rapide aridification du climat. Les données de terrain révèlent qu'une extinction en masse affecte 69 % des vertébrés terrestres à la fin du Permien, la durée de l'événement s'étalant sur environ 300 000 ans avant la PTB. Elle est suivie par un événement de moindre ampleur, avec un taux d'extinction de 39 %, survenant approximativement 160 000 ans plus

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tard et comportant quatre taxons survivant au passage de la PTB. Les faunes de la reconquête du Trias inférieur comprennent des archosauromorphes protérosuchiens (*Proterosuchus*), de petits amphibiens (*Micropholis, Lyddekerina*), de petits procolophonidés (*« Owenetta » kitchingorum, Procolophon*), des dicynodontes de taille moyenne (*Lystrosaurus*) et de petits cynodontes insectivores (*Progalesaurus, Galesaurus, Thrinaxodon*). Les distorsions taphonomiques, en privilégiant la préservation des fossiles dans les mares en voie d'assèchement du début du Trias, ont probablement fait surestimer l'abondance et la diversité des animaux amphibies ou fouisseurs. ***Pour citer cet article : R. Smith, J. Botha, C. R. Palevol 4 (2005)***.

Keywords: Terrestrial vertebrates; Mass extinction; Recovery; Permo-Triassic boundary (PTB); Karoo Basin; South Africa

Mots clés : Vertébrés terrestres ; Extinction en masse ; Reconquête ; Limite Permien-Trias ; Bassin du Karoo ; Afrique du Sud

1. Introduction

The end-Permian mass extinction that occurred at approximately 251 Ma [8] is generally regarded as the most catastrophic of the five major Phanerozoic mass extinctions. An estimated 90% of all marine species (e.g. [5,17,33,50]) and 70% of all terrestrial vertebrate families [34,35] disappeared within 165 kyr [8] and perhaps as little as 10 kyr [56,60]. Research to date on the Permo-Triassic boundary (PTB) has focused more on patterns of taxon extinctions and possible causes for the extinction event (e.g., [2,3,22,24,47,60]) rather than on the recovery of biodiversity during the Early Triassic. Numerous marine PTB sections have provided a broad indication of the devastation of marine life [22,24,25,36,60]. However, the details of the effect of the end-Permian extinction on the terrestrial ecosystems of Pangaea remain poorly understood. Worldwide there are very few stratigraphic sequences that are complete enough to preserve the terrestrial end-Permian mass extinction and the succeeding Early Triassic recovery. One of these rare locations is the South African Karoo Basin, where recent work has revealed a complete terrestrial sequence from the Permian to the Triassic, containing abundant fossils that record changes in floral and vertebrate taxa across the PTB and subsequent recovery of the southern Gondwanan ecosystems in the Early Triassic [52,53].

Over the past ten years, 225 in situ vertebrate fossils have been systematically collected from the PTB sequences in the Bethulie and the Graaff-Reinet districts of the southern and central Karoo Basin (Fig. 1). Here, we present a compilation of the latest palaeoenvironmental and biostratigraphic data collected from these sections with particular emphasis on the nature and the controls of the recovery of Early Triassic terrestrial vertebrate communities after the end-Permian mass extinction.

2. Palaeoenvironment

The Karoo Supergroup is a thick succession of sedimentary rocks that accumulated in a large, intracratonic, retroarc foreland basin in southwestern Gondwana. The strata record more than 100 Ma of almost continuous sediment accumulation from the Permo-Carboniferous (300 Ma) through to the Early Jurassic (190 Ma) under a range of climatic regimes and within several tectonically controlled sub-basins.

From the Middle Permian onwards, some 4000 m of vertebrate-fossil-bearing fluvio-lacustrine sediments that make up the Beaufort Group dominate the Karoo Supergroup succession. The PTB occurs in the middle of the Beaufort Group succession and is not only marked by a major extinction episode, recorded in the fossil record by the '*Glossopteris-Dicroidium* floral succession' and the therapsid fauna, but also coincides with a major change in fluvial style.

2.1. Sedimentology of the PTB sequence

The main extinction zone is approximately 40 m thick at both the Bethulie and the Graaff-Reinet sections and is stratigraphically positioned in the lower strata of the Palingkloof Member at the top of the Balfour Formation (Fig. 1). Detailed sedimentological logs compiled from several sections at each locality show that the facies sequences in the boundary beds are remarkably similar (Fig. 2). The overall lithological transitions are from drab greenish grey and blue-grey thickly-bedded and pedogenically modified massive

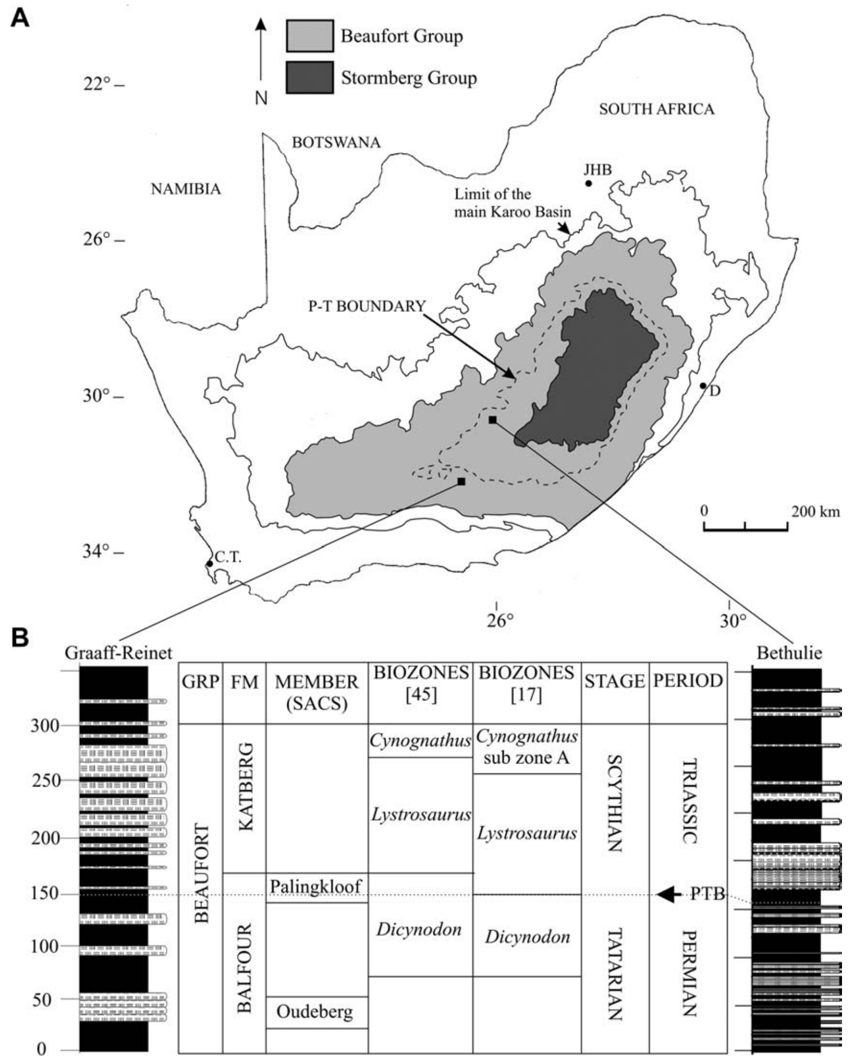

Fig. 1. (**A**) Map of South Africa, showing the location of Bethulie and Graaff-Reinet districts where detailed lithostratigraphical sections were conducted. (**B**) Summary of the litho- and biostratigraphy for the southern and central Karoo Basin indicating the stratigraphic positions of the PTB described in this report. Abbreviations: C.T., Cape Town; D, Durban; JHB, Johannesburg; SACS, South African Committee for Stratigraphy.

Fig. 1. (**A**) Carte d'Afrique du Sud localisant les districts de Bethulie et de Graaff-Reinet, où des coupes lithostratigraphiques détaillées ont été relevées. (**B**) Synthèse des données litho- et biostratigraphiques des parties méridionales et centrale du bassin du Karoo, indiquant les positions stratigraphiques de la PTB décrites dans cet article. Abréviations : C.T., Le Cap; D, Durban; JHB, Johannesburg; SACS, Comité sud-africain de stratigraphie.

siltstone beds with interbedded, laterally-accreted fine grained sandstone bodies grading upwards into progressively more maroon coloured siltstone beds interbedded with vertically accreted sandstones with distinctive gullied basal scours and include a regionally extensive interval of maroon coloured thinly bedded laminites. The PTB sequence is capped by a thick conglomeratic sandstone-dominated succession – the Katberg Formation.

2.1.1. *Massive dark grey mudrock*

In the drab-coloured dark grey (5Y 4/1) and olive grey (5Y5/2) mudrocks below the PTB, large dark brown weathering calcareous nodules and claystone

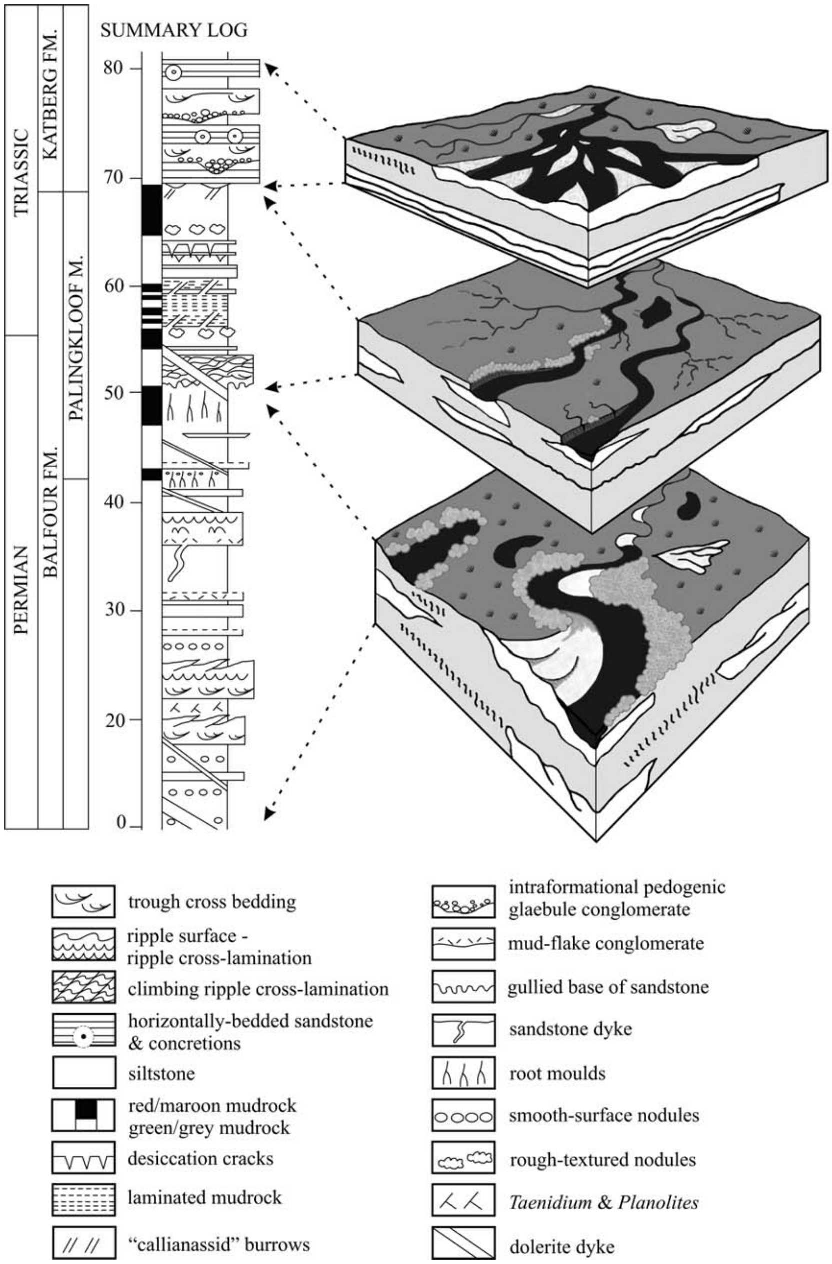

Fig. 2. Summary sedimentological log of the PTB sequence compiled from the study sections in the Bethulie District with interpreted palaeo-landscape reconstructions. Vertical scale in metres.
Fig. 2. Profil sédimentologique synthétique de la séquence de la PTB, d'après les coupes étudiées dans le district de Bethulie et interprétations des paysages correspondants. Échelle verticale en mètres.

lined-root channels as well as *Planolites* and *Taenidium* burrows are evidence for several extended periods of stasis and soil formation in the floodplain. Vertebrate fossils are relatively rare in these strata and comprise disarticulated postcranial bones of medium and large dicynodonts, lower jaws and isolated skulls. This interval has an unusually high incidence of skull fragments, especially isolated caniniform processes of tusked dicynodonts. Approaching the PTB, beds of dark red (10R 3/6) mudrock appear in the succession, becoming thicker and more reddish brown in colour until this facies dominates the succession.

2.1.2. Maroon laminites

At both localities, and possibly throughout the southern Karoo Basin [56], the last occurrence of *Dicynodon* (marking the biostratigraphic PTB) coincides with an interval of rhythmically-bedded laminated mudrock containing a single horizon of large brown weathering calcareous nodules. This facies comprises a distinctive succession of thinly bedded dark reddish–brown (2.5YR3/4) and olive–grey (5Y5/2) siltstone/mudstone couplets. As with all the mudrock colours, they are very sensitive to contact metamorphism such that close to dolerite intrusions, the maroon colour of the laminites is converted to light grey. Upper surfaces of the centimetre-thick siltstone beds commonly display small oscillation ripples and some pustular textures that resemble the impressions of algal mats. This facies has very little evidence for pedogenesis, however, Retallack et al. [48] figure hollow roots of aquatic isoetaleans from this interval and it does have distinctive long cylindrical unbranched callianassid-like burrow casts with possible scratch marks on the outer surface. At the Bethulie locality very rare fossils of *Lystrosaurus maccaigi* and *Moschorhinus* have been recovered from this interval.

2.1.3. Massive red siltstone facies

Above the laminated beds at both localities, the section comprises massively bedded red (2.5YR4/6) and olive-grey siltstone interbedded with minor thin gullied sandstone sheets and horizons of sand-filled mudcracks. Large dark reddish brown weathering calcareous nodules occur isolated and along horizons within the red siltstone beds. Lenses of reworked pedogenic glaebules fill the gullies on the basal surfaces of some of the sandstones. Articulated *Lystrosaurus* skeletons become relatively abundant in this interval and are commonly thickly enveloped in calcareous nodular material. The callianassid-type cylindrical burrows are also present in this interval.

2.1.4. Conglomeratic sandstone facies

At both localities, the massive red siltstone facies is terminated by the base of the Katberg Formation, a sandstone-dominated succession composed of stacked tabular light olive grey (5Y6/2) fine-grained sandstone bodies containing numerous scoured disconformities lined with lenses and stringers of intraformational mud pebble and glaebule conglomerate. A diagnostic feature of these sandstone bodies is the ubiquitous occurrence of spherical to ovoid brown-weathering calcareous concretions with septarian shrinkage cracks in the core.

2.2. Interpreted palaeoenvironmental changes across the PTB

The facies sequence through the PTB is interpreted as a relatively rapid change in fluvial landscape from an alluvial plain traversed by a few large, highly meandering rivers with expansive lowland floodplains (*massive dark grey mudrock*) through a transitional stage when the rivers straightened and branched into a distributary channel network that scoured the now abandoned floodplains (*massive red siltstone*) [52]. The field evidence of more flashy discharge in the Triassic is the appearance of distinctive gullies at the base of the channel sandstones filled with reworked pedogenic nodules and large mudrock rip up clasts. The rapid switching of the talweg within a wide, low sinuosity channel is indicated by the numerous vertically-stacked sheet sandstones with glaebule conglomerate-lined disconformities. It has been proposed that this switch in fluvial style was triggered primarily by the die-off of bank strengthening vegetation [55]. As the run-off charged sediment load increased, these channels widened and in-channel bars eventually separated the flow into a braided pattern of interconnected sand-dominated ephemeral channels (*conglomeratic sandstone*). During deposition of the massive red siltstone facies, there was an apparently synchronous depositional event that immediately followed the extinction of *Dicynodon* – the last of the Permian dicynodonts to disappear from the Karoo Basin. This resulted in the accumulation of up to 5 m of finely laminated mudrocks (*maroon laminites*) that show evidence of shallow standing water with periodic sub-aerial exposure and desiccation. Thin sections of the laminae show light dark alternations that may be interpreted as varves and suggest accumulation within a thermally stratified standing water body which in this climatic setting would be termed a playa lake [48]. Periodic flooding deposited sand/mud couplets that show little post-depositional colonization by either animal or plant life except minor root traces of a hydrophilic quillwort [48], and burrows of a possible crustacean. The conclusion drawn from this evidence is that for a short period following the disappearance of *Dicynodon*, the central Karoo Basin floodplains were almost devoid of vegetation, and were seasonally occupied by widespread playa lakes. Using the average floodplain accretion rate of 1.5 mm calculated by Retallack et al. [48] from the weak palaeosol development in the laminites, applying a 60% compaction ratio [1] and adding two short periods of pedogenesis, gives an estimated time interval for the 5m thick laminites as approximately 10 000 years.

Above the laminites, the floodplain accretion rates decrease and pedogenic overprinting is again evident, except the palaeosol character has changed. The massive red siltstone beds are interpreted as having been initially deposited by overbank flood events but subsequently re-worked by wind action as loess [52]. The palaeosols, although distinctively red in colour, have a slightly greater depth to calcic horizon than those of the Latest Permian. Retallack et al. [48] interpret this as a modest increase in seasonal precipitation from an estimated 346 mm to 732 mm across the boundary, combined with an increase in mean annual temperature and a change in vegetation type from an arid *Glossopteris* dominated flora to a semi-arid equisetalian flora. Perhaps a more plausible interpretation of the observed changes in fluvial style and pedogenesis is that they were brought about by an increase in mean annual temperature combined with the onset of a monsoonal rainfall regime [48]. Within a completely continental setting such as the Karoo Basin, this resulted in more highly seasonal rainfall and increased storm intensity, but with lower reliability.

2.3. Taphonomy of the PTB: evidence for drought accumulations

The fossils show a pattern of disappearance and a taphonomic mode that suggests that drought may have been a contributing factor to the extinctions. At the beginning of the main period of extinction a new dicynodont genus, *Lystrosaurus*, first appeared in the basin as rare large isolated skulls and skeletons of the long-nosed *Lystrosaurus maccaigi.* This new arrival co-existed with the gradually dwindling *Dicynodon* fauna for an estimated 250–425 kyr (40 m of floodplain strata corrected for 60% compaction and accumulated at an estimated 0.15–0.25 mm yr^{-1} [48]) before *Dicynodon*, the last remnant of the Permian fauna, finally went extinct. By the time the last of the *Dicynodon* disappeared *Lystrosaurus* had already become the most common large vertebrate in the basin, yet it was not until between 7.5 and 22.5 kyr later (7 m above the PTB with 60% compaction ratio and accumulation rates of 0.5–1.5 mm yr^{-1} [48]) that the rest of the *Lystrosaurus* Assemblage Zone recovery fauna became abundant enough to be preserved in the rock record. The field evidence shows that the small dicynodonts disappeared before the medium and large herbivores, which suggests that their food source, presumably the undergrowth of lush ferns and clubmosses, disappeared before the *Glossopteris* shrubs and trees. This is in keeping with the sedimentological interpretation of the lowering of water tables and the onset of drought conditions. The fact that the medium- and large-sized *Lystrosaurus* seemingly flourished as the *Dicynodon* fauna began to fade, indicates that it was somehow pre-adapted to survive the worsening conditions. This is discussed more fully further in this report.

Several ‘bonebeds’ comprising numerous (±10) jumbled-up disarticulated sub-adult *Lystrosaurus* skeletons occur in the maroon floodplain mudrocks of the Lower Triassic Katberg Formation (Fig. 3). They are interpreted as drought induced aggregations where animals died *en masse* on the periphery of a shrinking waterhole. Subsequent, possibly monsoonal, downpours resulted in short-lived sheet washes that transported the desiccated bones into shallow depressions along with reworked cohesive mud clasts and nodules [53,54].

2.4. Causes of the end-Permian mass extinction

The changes in fluvial style in the Karoo Basin at the end of the Permian were initially thought to be triggered by a pulse of thrusting in the southerly source area, which brought about rapid progradation of a large sandy braided fan system (the Katberg Fm.) into the central parts of the basin [21,52]. Ward et al. [55] suggested an alternative that better fits the observed palaeoclimatic changes. They proposed that the switch in fluvial regime was a consequence of the extinction event rather than the cause. The global aridification and con-

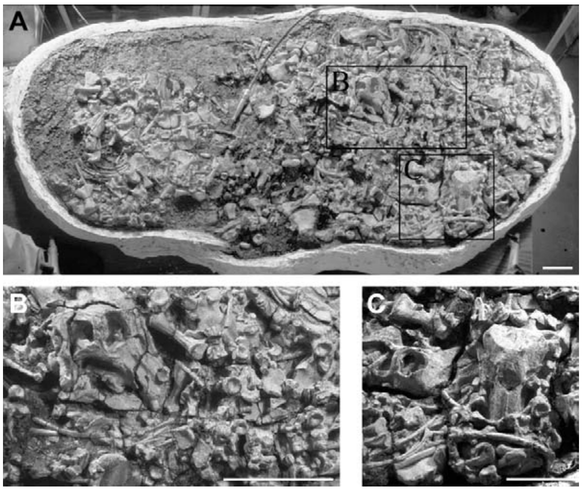

Fig. 3. *Lystrosaurus* bonebed recovered from the Lower Triassic Katberg Formation in the Bethulie District interpreted as a drought accumulation of ten sub-adult animals that died in and around a dried up waterhole/wallow. The corpses became desiccated before falling apart with negligible removal or breakage caused by scavengers. Less than two years later sheetwash from a thunderstorm swept then into the depression where they were buried then beneath a layer of silt. (**A**) Complete prepared bonebed – note its elongate shape filling a floodplain depression. (**B**) Detail of part of the *Lystrosaurus* bonebed showing a lateral-up *Lystrosaurus declivus* skull surrounded by disarticulated vertebrae, ribs and limb elements. (**C**) Detail of part of the *Lystrosaurus* bonebed showing two *L. declivus* skulls in amongst randomly scattered limb and vertebral elements. Scale bars equal 10 cm.

Fig. 3. *Bonebed* à *Lystrosaurus* provenant du Trias inférieur de la formation Katberg, dans le district de Bethulie, interprété comme résultant de la concentration de dix animaux sub-adultes morts lors de l'assèchement d'une mare ou d'une bauge (dans la nappe d'eau ou à proximité de celle-ci). Les cadavres furent préalablement soumis à dessiccation, la désarticulation et la fragmentation des squelettes par les organismes nécrophages demeurant négligeables. Moins de deux ans après leur mort, un ruissellement en nappe provoqué par un orage les a entraînés dans la dépression où ils furent ensevelis sous une couche de silt. (**A**) *Bonebed* après complet dégagement – noter sa forme allongée, épousant celle du remplissage d'une dépression de la plaine d'inondation. (**B**) Détail du *bonebed* à *Lystrosaurus*, montrant une vue latérale d'un crâne de *Lystrosaurus declivus*, entouré par des vertèbres désarticulées et par des fragments de pattes et de côtes. (**C**) Détail du *bonebed* à *Lystrosaurus*, montrant deux crânes de *L. declivus* parmi des fragments de pattes et de vertèbres éparpillés au hasard. Barres d'échelle = 10 cm.

comitant de-vegetation of the continental interiors caused unstable channel banks and increased run-off that is reflected by the onset of gullying of the floodplains and the switch from high to low sinuosity channel pattern.

Stable isotopic analyses of pedogenic nodules and teeth taken from embedded fossils through the extinction interval at the Bethulie section revealed an anomalous negative excursion within the boundary laminites [34,56]. This anomaly is interpreted as having been caused by a relatively rapid release of methane or CO_2 into the atmosphere over a period of some 150 kyr. The greenhouse effect from these emissions, whether they originated from the Siberian volcanism [47] or oceanic overturn [32], could have caused the observed global aridification of continental interiors [48].

3. Recovery fauna

To date, 225 in situ fossils representing a total of 23 vertebrate taxa have been recovered from the terrestrial PTB sections in the southern and central Karoo Basin. Of these 23 taxa, nine became extinct within the uppermost 40 m of Permian strata (estimated mean duration of 300 kyr based accretion rates calculated from pedogenesis [48]), four survived the extinction for an estimated 160 kyr before disappearing (< 30 m above PTB) and ten taxa originated during the Earliest Triassic recovery phase (7–47 m above PTB, see Fig. 5), which is estimated to have lasted some 250 kyr. As a group, the dicynodonts were the hardest hit by the extinction event with an 83% generic extinction rate, although *Pristerodon* went extinct relatively early compared to the rest of the other dicynodonts and was possibly not part of the extinction event itself.

Out of the 13 taxa recovered from the Latest Permian portion of the PTB sections in South Africa, only four genera (31%) survived the extinction: the dicynodont *Lystrosaurus* and the therocephalian genera *Tetracynodon, Moschorhinus* and *Ictidosuchoides.* However, none of the therocephalian genera survived into the succeeding Early Triassic Katberg Formation, because they died out in the upper Palingkloof some 160 kyr after the main extinction event during what could be interpreted as a second pulse of extinctions amongst the 'survivor fauna' (Fig. 5).

Out of the ten taxa recovered from Earliest Triassic strata, directly above the PTB, seven taxa originate within 30 m of the boundary. The first new taxon to appear almost immediately above the boundary (at approximately 7 m) is the archosauriform *Proterosuchus* sp. This taxon is closely followed by the amphibian *Micropholis* sp. and the procolophonoid *'Owenetta' kitchingorum* (soon to be placed in a new genus [41]), the dicynodonts *Lystrosaurus murrayi* and *L. declivis*, and the cynodonts *Thrinaxodon liorhinus* and *Galesaurus*. The amphibian, *Lydekkerina* sp., the procolophonoid *Procolophon* sp. and the therocephalian *Scaloposaurus* sp. appear stratigraphically higher in the Katberg Formation, with *Lydekkerina* appearing first at approximately 37 m above the boundary. *Procolophon* was previously regarded as originating just above the PTB [49], but our collecting has repeatedly shown that this taxon makes its first appearance approximately 60 m above the PTB, thereafter it then occurs in abundance.

3.1. Adaptive radiation of the recovery fauna

The collecting data shows that the archosauriform, *Proterosuchus*, is the first vertebrate taxon to appear in the Karoo Basin following the End-Permian mass extinction (Fig. 5) and, as such, can be regarded as the terrestrial index fossil for the Early Triassic in South Africa. Unlike *Moschorhinus*, which survived the main extinction event only to disappear soon after, *Proterosuchus* first appears during the Earliest Triassic (at approximately 7 m above PTB) and extends well into the overlying Katberg Formation [49]. The reasons why *Proterosuchus* flourished and the similarly sized *Moschorhinus* declined may be due to lifestyle differences. An amphibious lifestyle is regarded as ancestral for all archosauromorphs, thus, it is likely that the archosauriform *Proterosuchus* was at least semi-aquatic, and therefore, may have lived in and around the more permanent water bodies. If this is the case, *Proterosuchus* too would have become part of the preferential preservation of skeletons in and around ephemeral ponds and lakes.

The amphibian genus *Micropholis* first appears in the fossil record at approximately 18 m above the PTB. These specimens have often been found in association with the procolophonoid *'Owenetta' kitchingorum*. The species *'Owenetta' kitchingorum* is widely thought to extend the range of the genus from the Permian into the Triassic (e.g., [51]), but recent studies indicate that it should be placed in another or its own genus [14,40]. When this is done, it will result in the absence of *Owenetta* from the Triassic.

Currently, there are thought to be three Late Permian cynodont genera in the South African Karoo Basin, viz. *Procynosuchus, Cynosaurus*, and *Nanictosaurus* [49]. However, our collecting data shows that none of these genera cross the PTB. Three new genera appear in the Earliest Triassic, in the upper Palingkloof Member of the Balfour Formation. They include *Progalesaurus* [51], *Galesaurus* and *Thrinaxodon liorhinus* (Fig. 5). *Progalesaurus*, the sister taxon of *Galesaurus*, was recently recovered from the Earliest Triassic Palingkloof Member, approximately 36 m above the PTB [51]. It is currently represented by a single type specimen and, thus, has not been plotted on the range chart in Fig. 5.

4. Discussion

4.1. Patterns of faunal extinction, survival and recovery at the PTB

The biostratigraphical field data shown in Fig. 5 indicates that of the seven Late Permian dicynodont taxa recovered from the PTB sections in South Africa, only one taxon, *Lystrosaurus curvatus*, actually survived the extinction. In contrast, our fossil recovery shows that 75% of the Late Permian therocephalian genera survived the extinction. However, to date, we have not found a single Late Permian amphibian, eosuchian, procolophonoid or cynodont genus that survived into the Earliest Triassic portion of the Palingkloof Member in the South African Karoo Basin, although new genera representing all these groups appear later in the Early Triassic strata of the Katberg Formation.

The dicynodonts were clearly more affected by the end-Permian extinction compared to any other therapsid clade, apart from the Gorgonopsia, which are absent from the Early Triassic. Of the nine gorgonopsian genera found in the lower *Dicynodon* Assemblage Zone, our collecting shows that only two are represented in the uppermost strata, suggesting that the gorgonopsians were in decline well before the end of the Permian [29]. The dicynodonts on the other hand were still relatively diverse and abundant during the latest Late Permian, but were almost completely eradicated during the end-Permian extinction event (although it should be noted that of the eight dicynodont genera present at the time of the *Dicynodon* Assemblage Zone, only five persisted up to the PTB beds). To date, the field data show that the only dicynodont taxon represented on both sides of the PTB in South Africa is *Lystrosaurus curvatus.* At present, it can be regarded is a boundary interval marker as its narrow range is restricted to approximately 20 m, spanning the boundary interval itself (Fig. 5, [7]).

Along with *Lystrosaurus curvatus*, the therocephalian genera *Ictidosuchoides, Moschorhinus* and *Tetracynodon* also survived the end-Permian extinction event. *Moschorhinus* is the only large terrestrial carnivore (apart from the archosauriform *Proterosuchus*) present during the Earliest Triassic. However, none of these four surviving taxa have been found above the Earliest Triassic portion of the Palingkloof Member of the Balfour Formation, and although they survived the extinction, they do not appear to have flourished during the Early Triassic as all four taxa disappear within 30 m of the PTB (Fig. 5, [16]).

The recovery taxa are all new genera that have not been found in Late Permian strata. Archosauriforms are the first group to appear in Earliest Triassic strata, closely followed by amphibians, procolophonoids, dicynodonts and then cynodonts. These taxa clearly had adaptations/lifestyles that allowed them to flourish on the arid braidplains of the Early Triassic Karoo Basin. It is noteworthy that the recovery in South Africa was faster compared to that in the South Urals basin in Russia [6,20]. Benton et al. [5] noted that small fish-eaters and insectivores were absent from the Early Triassic in the South Urals basin after the end-Permian extinction event, whereas aquatic nymph eaters such as *Micropholis* and insectivores such as *Galesaurus* and *Thrinaxodon* appear much sooner after the extinction event in South Africa.

4.2. Early Triassic faunal habits and habitats

Currently there are four taxonomically valid *Lystrosaurus* species in South Africa: *L. maccaigi, L. curvatus, L. murrayi* and *L. declivis* [18]. *Lystrosaurus curvatus, L. murrayi* and *L. declivis* are the only dicynodont species present in the Earliest Early Triassic (Fig. 5). The rest of the dicynodonts including the other *Lystrosaurus* species, *L. maccaigi*, became extinct at or immediately below the PTB. Although *Lystrosaurus curvatus* survived the extinction event, it disappeared soon after the extinction. In contrast, *L. murrayi* and *L. declivis* flourished after the extinction to become two of the most abundant and successful herbivores during the Early Triassic. It is clear that *L. murrayi* and *L. declivis* as well as the small cynodonts, small amphibians and small procolophonoids were well-adapted to the Early Triassic Karoo environment and had morphological adaptations and/or lifestyles that allowed them to flourish in relatively arid conditions [52]. Several survival strategies have been proposed over the years and the various theories are summarised below.

4.2.1. Drought-tolerant food source

King and Cluver [30] examined the *Lystrosaurus* skull and found that it was modified for eating tough or resistant plant matter (massive snout; strong lower jaw symphysis, zone of weakness in the nasal region; retention of cartilage in various regions of the skull, shortened skull; down-turned snout; heightened temporal area). Smith [52] proposed that *Lystrosaurus* may have been pre-adapted to feeding on tough stemmed horsetails, which survived the end-Permian extinction event because of their drought resistance and generally aquatic habitat [45]. Quillworts such as *Isoetes*, may also have been an important food source as their remains have also been found associated with *Lystrosaurus*l. Quillworts and horsetails live today in water or in wet meadows [48]. *Lystrosaurus curvatus* may, therefore, have survived the extinction purely because its primary food source did so as well.

4.2.2. Fossorial lifestyle

Anatomical features of the humerus and the spatulate construction of the claws suggest that *Lystrosaurus murrayi, L. declivis* [30] and possibly *L. curvatus* (personal observation) may have burrowed beneath the Early Triassic floodplain to escape harsh environmental conditions. This is supported by the presence of some articulated *Lystrosaurus* remains preserved in sand-filled burrow casts within floodplain mudrocks of the Katberg Formation [7,19,37,48].

Although all the Earliest Triassic cynodonts are all new genera, there is no decrease in diversity, suggesting that the cynodonts were not as adversely affected by the extinction compared to the dicynodonts. Recent research has suggested that *Thrinaxodon liorhinus* [16] and *Galesaurus* (Neveling, pers. commun. 2004) were either obligate burrowers or at least habitually inhabited burrows (Fig. 4). *Progalesaurus*, as the sister taxon of *Galesaurus*, is likely to have been a burrower as well.

Fig. 4. A pair of fully-articulated, juvenile *Thrinaxodon lihorhinus* lying in an attitude that strongly suggests they were preserved in a hibernation position at the end of an underground burrow. This specimen was recovered from a thick maroon siltstone bed 32 m above the PTB on Old Wapadsberg Pass in the Graaff-Reinet District. Scale bar equals 2 cm.

Fig. 4. Deux exemplaires juvéniles de squelettes de *Thrinaxodon lithorhinus* en connexion anatomique, disposés dans une attitude qui suggère fortement qu'ils ont été conservés dans une position d'hibernation à l'extrémité de leur terrier. Ces échantillons proviennent d'un épais lit de *siltstone* de couleur marron, situé à 32 m au-dessus de la PTB, sur l'Old Wapadsberg Pass, dans le district de Graaff-Reinet. Barre d'échelle = 2 cm.

Such a predominance of burrowing in the Earliest Triassic cynodonts suggests that this life habit played a significant role in allowing these cynodonts to tolerate the Early Triassic aridification of southern Gondwana. Retallack et al. [48] suggested that a fossorial lifestyle may have also pre-conditioned the burrowers to survive high carbon dioxide and low oxygen levels during the end-Permian extinction event.

4.2.3. Amphibious lifestyle

A semi-aquatic, amphibious lifestyle was originally suggested for *Lystrosaurus* by Robert Broom [10], an interpretation later supported by numerous authors [9,12,15,23,26,31,57,58]. A review of *Lystrosaurus* by King [28] and King and Cluver [30] opposed the aquatic lifestyle view and instead suggested that *Lystrosaurus* adopted a fully terrestrial lifestyle and was capable of burrowing into parched floodplain soils to regulate temperature and humidity. Recently, the amphibious *Lystrosaurus* hypothesis has been resurrected by Ray et al. [44], who cited a bone microstructure similar to semi-aquatic animals.

Alternatively, the over abundance of *Lystrosaurus* specimens in the Early Triassic Karoo strata may be a taphonomic bias caused by preferential preservation of drought accumulations. The anomalous occurrence of monospecific *Lystrosaurus* bonebeds in the post extinction semi-arid floodplains of the Katberg Formation suggests that standing water bodies became the aggregation areas for Early Triassic biodiversity. However, it appears that the floodplain ponds and lakes were susceptible to periodic drying and thus, the associated flora and fauna were also subjected to periodic die-off. The combination of lowland floodplain 'waterholes' and periodic die-off are ideal sites for the accumulation and burial of bones [59]. The evidence for waterhole setting is the fact that the bonebeds are hosted by pedogenically modified floodplain strata with no indication of channel form, the matrix comprises locally derived mud pebble and clay chip conglomerate, the geometry of the bonebeds is dish-shaped as if lining the floor of a floodplain depression and there is evidence for rapid drying of the carcasses before burial. It is possible therefore that the apparent "water dependence" [42] of the Early Triassic recovery fauna in the Karoo Basin may be a taphonomic bias caused by the preferential preservation of drought accumulations around ponds and lakes.

4.3. Ghost lineages versus a direct reading of the fossil record

Although the amphibians *Micropholis* and *Lydekkerina*, the archosauriform *Proterosuchus*, the procolophonoids *'Owenetta' kitchingorum* and *Procolophon*, and the cynodonts *Thrinaxodon liorhinus* and *Galesaurus* appear to originate in Earliest Triassic strata, it is argued that there must have been at least seven separate ghost lineages that crossed the boundary to give rise to these taxa [14,41,51]. *Lystrosaurus murrayi* and *L. declivis* appear to be very closely related taxa [18] and may have evolved from a Triassic *L. curvatus* type ancestor (although the relationships between the various *Lystrosaurus* species using cladistic analysis require examination). With the addition of ghost lineages to our field data, 48% of all taxa cross the PTB in the Karoo Basin, but out of these taxa only four genera (17%) actually cross the boundary. Furthermore, these four genera, *Lystrosaurus* (*curvatus*), *Ictidosuchoides, Tetracynodon* and *Moschorhinus*, disappear close to the boundary in the Earliest Triassic portion of the Palingkloof Member in what could be described as a second wave of extinctions.

Recent work based on the existence of ghost lineages, led Modesto et al. [41] to suggest that the effect

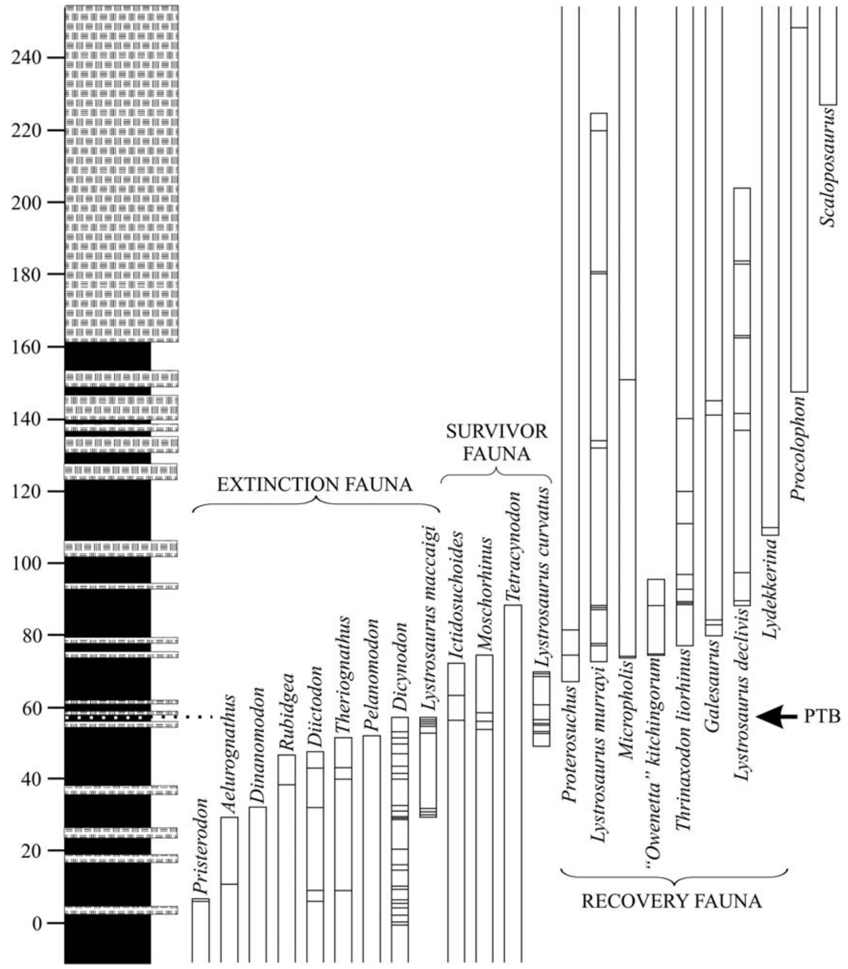

Fig. 5. Range chart of terrestrial vertebrate fossils found in situ in the PTB sequences of the southern and central Karoo Basin of South Africa and grouped into discrete extinction, survival and recovery faunas. The conversion of stratigraphic metres to the time estimates used in the text are based on floodplain accretion rate of 2 mm yr^{-1}, with an average compaction ratio of 50% and a compensation factor of × 5 to account for periods of non-deposition (pedogenesis) and erosion.

Fig. 5. Diagramme répertoriant la distribution des Vertébrés terrestres fossiles trouvés in situ dans les séquences de la PTB des régions méridionale et centrale du bassin du Karoo, en Afrique du Sud. Les faunes sont regroupés en trois catégories : extinction discrète, faunes survivantes et faunes de la reconquête. La conversion des épaisseurs des unités lithostratigraphiques en estimations de durée, utilisée dans le texte, est basée sur un taux d'accrétion de 2 mm an^{-1} dans la plaine d'inondation, avec un rapport moyen de compaction de 50% et un facteur de compensation de × 5 pour rendre compte des périodes de non-dépôt (pédogenèse) et d'érosion.

of the end-Permian extinction on terrestrial vertebrates was not as great as previously thought (e.g., [5,17,25,43]). Their studies on Late Permian and Early Triassic parareptiles from the Karoo Basin [38–41,46] have indicated that their survivorship rate may be as much as 71% [41]. This estimation was based on a study of six parareptile species including *Barasaurus besairiei, Owenetta rubidgei, Saurodectes rogersorum, 'Owenetta' kitchingorum, Coletta seca, Sauropareion anoplus* and the family Procolophonidae. Although *Saurodectes, "Owenetta" kitchingorum, Coletta*, and *Sauropareion* have only been recorded from Lower Triassic strata, a phylogenetic analysis shows that all four of these taxa have ghost lineages that must have crossed the PTB [41]. The lineages of *Coletta* and *Sauropareion*, which are transitional forms between Owenettidae and Procolophonidae [14] and whose ranges are based on single specimens, share a common ancestor with the Procolophonidae [14,41]. The ranges of all three taxa extend into the Late Permian on the basis of two Russian procolophonoids, namely, *Suchonosaurus* and *Kinelia*, based on a maxilla and a dentary, respectively [11]. More recently, the Permian *Barasaurus besairiei* from Madagascar has been shown to cross the PTB as well [27], which would suggest a parareptile survival rate of 86% (six out of seven taxa).

However, according to our field data of the first appearance datum of *'Owenetta' kitchingorum* (Fig. 5), it is possible that the common Late Permian ancestor (ghost taxon) of *Saurodectes* and *'Owenetta' kitchingorum* [14] crossed the PTB before separating into the two distinct genera (also mentioned as a possibility in [40]). This would result in *Barasaurus*, the ghost taxon of *Saurodectes* and *'Owenetta' kitchingorum, Coletta, Sauropareion* and the Procolophonidae crossing the PTB, which amounts to a 71% survival rate and agrees with Modesto et al. [41]. It should be noted, however, that no procolophonid has been found in the Late Permian Karoo Basin of South Africa. It is possible that, in the Karoo Basin, only three lineages (50%), namely, *Coletta seca, Sauroparieon anoplus* and the ghost taxon of *Saurodectes rogersorum* and *"Owenetta" kitchingorum* crossed the PTB.

It is clear from our field data that there was a massive faunal turnover at the PTB in the Karoo Basin with the number of actual genera crossing the boundary being extremely low (only 17%) and no fewer than nine new taxa (41%) appearing during the Earliest Triassic. A mass extinction is commonly defined as having a 40% extinction rate (e.g., [4,13]) and from our data, it can be seen that nine out of 23 taxa do not cross the PTB, which is equivalent to 39%. Thus, even when ghost lineages of the Earliest Triassic taxa are considered, the end-Permian extinction in the South African Karoo Basin still qualifies as a mass extinction.

It can be concluded that the taxa that are first recorded from Earliest Triassic strata (and whose lineages may have arisen during the Latest Permian) were in some way pre-adapted to the increasingly arid environment. These taxa include the archosauriform *Proterosuchus*, the amphibians *Micropholis* and *Lydekkerina*, the parareptiles *'Owenetta' kitchingorum* and *Procolophon*, the dicynodonts *Lystrosaurus murrayi* and *L. declivis*, and the cynodonts *Thrinaxodon liorhinus* and *Galesaurus*, all of which may have adopted either burrowing or amphibious lifestyles [30]. Thus, it is possible that both fossorial and amphibious lifestyles enabled terrestrial vertebrates to flourish in the Earliest Triassic continental environments of Gondwana.

5. Conclusions

Detailed biostratigraphic and sedimentological logging of two widely spaced PTB sections in the central and southern Karoo Basin of South Africa has allowed the following conclusions to be made about the geomorphological and ecological changes that took place during and after the mass extinction.

1. Field data demonstrate a 69% mass extinction of Late Permian terrestrial vertebrates lasting approximately 300 kyr and terminating at the PTB, followed by a lesser extinction pulse (31%) involving all four survival taxa, approximately 160 kyr later in the Early Triassic.
2. The following Early Triassic recovery fauna comprises proterosuchian archosauromorphs (*Proterosuchus*), small amphibians (*Micropholis, Lydekkerina*), small procolophonoids (*'Owenetta' kitchingorum, Procolophon*), medium-sized dicynodonts (*Lystrosaurus*) and small faunivorous cynodonts (*Progalesaurus, Galesaurus, Thrinaxodon*).
3. Ghost lineage correction data applied to the phylogenies of these new Early Triassic taxa still result in an extinction event, but of lesser impact at 39% rather than 69%.
4. Taphonomic bias towards preferential preservation of drought accumulations in the Early Triassic fossil record may have over-emphasized the abundance and the diversity of semi-aquatic and burrowing animals and underrepresented the fauna that lived independently of water bodies.
5. Taphonomic observations of cynodont fossils suggest that they either excavated their own burrows or were habitual occupiers of underground burrows excavated by other vertebrates – this may have been a behaviour that allowed them to cope with the periods of drought in the monsoonal climate of the Earliest Triassic Karoo Basin.
6. From the facies interpretation and taphonomic data it is proposed that pronounced climatic warming and increased seasonality and storminess at the onset of an unreliable, monsoonal rainfall regime contrib-

uted to the mass extinction of terrestrial vertebrates in southern Gondwana. This is congruent with previous work, which has suggested that the warming was as a result of greenhouse gases (methane and CO_2) emitted from basaltic eruptions in northern Pangaea around 251 Ma combined with a latent instability in the Earth's cyclic systems brought about by the coalescence of Pangaea.

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