# THE DICYNODONT *LYSTROSAURUS* FROM THE UPPER PERMIAN OF ZAMBIA: EVOLUTIONARY AND STRATIGRAPHICAL IMPLICATIONS

*by* G. M. KING *and* I. JENKINS

ABSTRACT. The skull of the dicynodont *Lystrosaurus* cf. *curvatus* is described from the Late Permian Madumabisa Mudstones of Zambia, in association with several Upper Permian genera. It demonstrates that the widespread *Lystrosaurus*, hitherto regarded as characteristic of the Lower Triassic, cannot be used in isolation as a biostratigraphical zone fossil. It appears that *Lystrosaurus* was a survivor of the Permo–Triassic extinction event, rather than a product of early Triassic diversification of other surviving forms. Its absence from the Upper Permian of South Africa suggests that it may have been an immigrant from further north.

The Upper Permian fauna of the Madumabisa Mudstones is comparable to that of the Upper Guodikeng Formation of China. The fauna is younger than that of the *Dicynodon* Assemblage Zone of South Africa, but may be contemporaneous with that of the Cuttie's Hillock Formation of Scotland.

THE anomodonts were a widespread, diverse and abundant group of mainly herbivorous therapsids (mammal-like reptiles) which lived in the Permian and Triassic (King 1990*b*). A recent study of their generic diversity at their acme in the Late Permian *Cistecephalus* Assemblage Zone (*sensu* Rubidge in press) of South Africa, suggested that approximately 15 genera were present (King 1993). This contrasts with the situation at the beginning of the Triassic (the *Lystrosaurus* Assemblage Zone) in South Africa, where only two genera *Lystrosaurus* and *Myosaurus* are known. Despite the paucity of genera in this assemblage, dicynodonts are nevertheless numerically abundant and hundreds of specimens have been collected from South Africa alone. The presence of more than one species of the genus *Lystrosaurus* is unusual for South African dicynodonts (King 1993), and could be linked to the dearth of other anomodonts of a similar size from the lowermost Triassic. The other genus of anomodont from the Lower Triassic, *Myosaurus*, was a very small animal, whereas *Lystrosaurus* was a medium-large anomodont. King (1991) and Cluver and King (1991) have shown that there is no firm evidence for the contention that *Lystrosaurus* was an aquatic or semi-aquatic animal, and so the reason for the success of *Lystrosaurus* is still to some extent a mystery.

Specimens of *Lystrosaurus* have been reported from South Africa, India, China, Antarctica, Russia, possibly Australia and, more doubtfully, Laos. Their occurrence is taken to indicate an earliest Triassic age for the horizons in which they have been found, and the genus has therefore been considered to be a useful stratigraphical marker. In the South African Permo-Triassic Karoo Basin, the genus is a zone fossil for the *Lystrosaurus* Assemblage Zone (Rubidge in press) and is considered to be confined to that zone. In it, *Lystrosaurus* is found most commonly together with the anapsid *Procolophon*, the diapsid *Proterosuchus*, the therocephalians *Moschorhinus*, *Scaloposaurus* and *Regisaurus*, and the cynodonts *Thrinaxodon* and *Galesaurus*.

Kemp (1976) described a collection of therapsid fossils from the Madumabisa Mudstones of the Luangwa Valley in Zambia. The composition of this assemblage indicates a latest Permian (*Dicynodon* Assemblage Zone) age for the localities. The following genera have been identified in the collection: *Dicynodon* (King 1981), *Oudenodon* (King 1979), *Procynosuchus* (Kemp 1979) and *Diictodon* (Gale 1988). Gorgonopsids and pareiasaur scutes are also present. A previously unidentified specimen in this collection is shown here to belong to the genus *Lystrosaurus*. This suggests either that *Lystrosaurus* occurs in the Upper Permian, or alternatively that several other genera of therapsids, hitherto regarded as Upper Permian, occur in the lowermost Triassic. It is

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more parsimonious to regard the *Lystrosaurus* specimen as being from the Upper Permian. No other genera typical of the Lower Triassic have been found in the Zambian collection.

### *Age of the Madumabisa Mudstones*

The presence of *Lystrosaurus* in the Upper Permian of Zambia may indicate that the age of the Madumabisa Mudstones is very near the Permo–Triassic boundary, and possibly significantly later than the South African *Dicynodon* Assemblage Zone. It also indicates that a mixed Late Permian–Early Triassic fauna existed in Zambia, similar to the transitional fauna proposed by Cheng (1993) for the Upper Guodikeng Formation in China (see below).

Some evidence for the greater age of the Zambian strata than those of South Africa is provided by the other dicynodonts of the Madumabisa Mudstones, in particular specimens of the genus *Dicynodon*. Several specimens in the Oxford University Museum TSK collection have a distinctive morphology which may indicate that they belong to a discrete species, probably *D. trigonocephalus* (King 1981). It is not possible to assert this with certainty, since the genus *Dicynodon* requires revision at the specific level. The distinctive features of these specimens are a medium-sized skull with breadth and length subequal giving a squarish dorsal profile; very abbreviated intertemporal region; short and deep basicranial region; and wide interorbital distance.

The dicynodont from Knock of Alves, Elgin, in Scotland (Benton and Walker 1985, p. 209), although only adequately preserved in the snout region, bears a marked resemblance to the Zambian *Dicynodon* specimens in general shape and morphology (GMK, pers. obs.). Benton and Walker considered that the age of the Cuttie's Hillock Formation at Elgin is also uppermost Permian. Walker (1973) tentatively suggested that the age might even be Lower Triassic. It would be interesting to determine whether *Lystrosaurus* Assemblage Zone strata are present in the Madumabisa Mudstones, and whether these might represent a continuous sequence through the Permo–Triassic boundary.

Institutional abbreviations for specimens referred to in this work are as follows: BMNH, Palaeontological Collections, The Natural History Museum, London; OUM.TSK, T. S. Kemp Collection, Oxford University Museum.

## SYSTEMATIC PALAEONTOLOGY

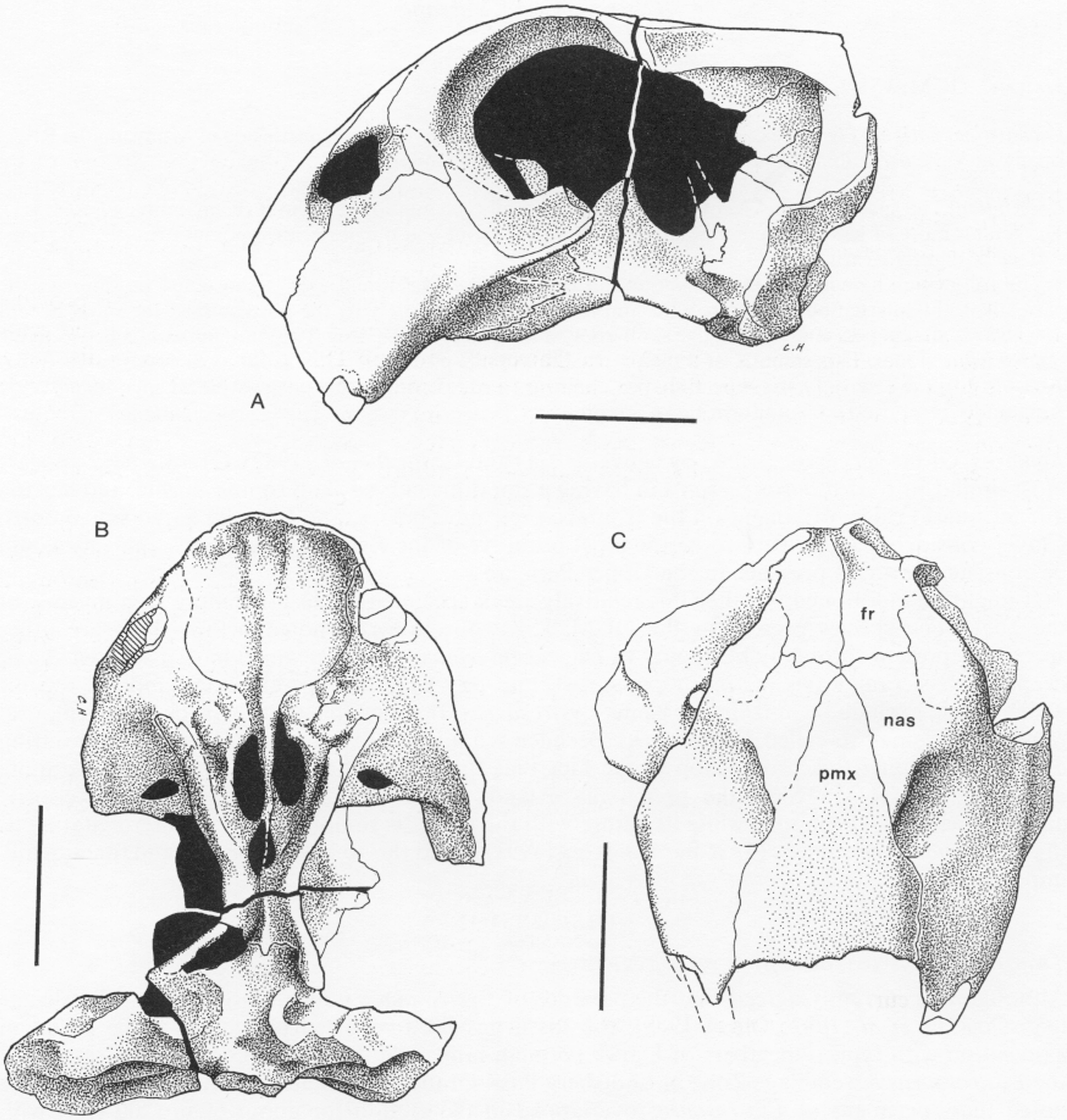
Subclass SYNAPSIDA Osborn, 1903
Order THERAPSIDA Broom, 1905
Infraorder DICYNODONTIA Owen, 1859
Superfamily PRISTERODONTOIDEA Cluver and King, 1983
Family DICYNODONTIDAE Cluver and King, 1983
Subfamily KANNEMEYERIINAE von Huene, 1948
Tribe LYSTROSAURINI Broom, 1903

Genus LYSTROSAURUS Cope, 1870

*Diagnosis*. Small to medium-sized dicynodont. Parietals widened; short snout, down-turned and deepened and formed by elongated maxilla and premaxilla; postcanine teeth absent; maxillary tusks present; orbits situated high on skull; nares immediately anterior to orbits; postfrontal present.

*Lystrosaurus curvatus* (Owen, 1876) Broom, 1932

*Holotype*. BMNH R3792, a skull; Elandsburg, Cradock, Cape Province, South Africa; *Lystrosaurus* Assemblage Zone, Lower Triassic.



TEXT-FIG. 1. *Lystrosaurus* cf. *curvatus*; OUM.TSK2; Late Permian Madumabisa Mudstones; Luangwa Valley, Zambia. A, left lateral view, solid black shading indicates matrix; a large crack runs dorso-ventrally through the skull. B, palatal view. C, anterior view. Abbreviations: fr, frontal; nas, nasal; pmx, premaxilla. Scale bar represents 40 mm.

*Diagnosis*. Snout not produced far ventrally; snout and tusk development weak; frontonasal and premaxillary ridges and frontal bosses absent; skull roof smooth; premaxillary plane curving over in a smooth arc to meet frontoparietal plane; frontal protuberances absent; suture between frontals and nasals lying in the frontoparietal plane; ventral ramus of squamosal extending posteriorly as well as laterally, concealing occipital condyles in lateral view.

### *Lystrosaurus* cf. *curvatus*

Text-figure 1A–C

*Material.* OUM.TSK2, a skull.

*Locality and horizon.* East side of hunter's track from Luangwa River, along north side of Munyamadzi River, Luangwa Valley, Zambia; Madumabisa Mudstones, Upper Permian.

*Description.* The specimen consists of a medium-sized skull (160 mm long) without the mandible (Text-fig. 1). The skull is more or less complete, but lacks the tip of the snout and the posterior zygomatic arches. The bone surface is slightly weathered.

The following characters of *Lystrosaurus* can be seen: the basicranial axis is shortened posteriorly; the parietals in the intertemporal bar are wide and not covered completely by the postorbitals; the snout is bent downwards making an angle with the skull roof, and is deepened (King 1990*b*). The suture between the premaxilla and maxilla is smooth, and the premaxilla extends posterodorsally as far as the prefrontals (pmx, Text-fig. 1C); the external naris is pear-shaped and bears a rugose ridge at its posteroventral edge (King 1991; King and Cluver 1991). Caniniform tusks are present.

*Remarks.* Of the species described by Cluver (1971) and Cosgriff *et al.* (1982), OUM.TSK2 appears most similar to *Lystrosaurus curvatus* in having a smoothly curved skull roof in profile, and lacking a fronto-nasal ridge, ornament on the frontals, prefrontal bosses, and laterally flared squamosals. Cluver considered *L. curvatus* to be the most primitive of the *Lystrosaurus* species and this would be consistent with its presence in the Upper Permian.

It might be questioned whether this relatively small specimen might not simply be a juvenile of the *Dicynodon* species present in the OUM.TSK collection. As noted below, there are other specimens present (probably belonging to *Dicynodon trigonocephalus*) which have a shortened and deepened basicranial axis (as in *Lystrosaurus*), but very narrow ridge-like intertemporal regions which would exclude them from the genus *Lystrosaurus*. It is possible that the wider intertemporal region of the small so-called *Lystrosaurus* specimen is a juvenile feature, becoming narrower during ontogeny. Against this proposition is the fact that the premaxillae of the two forms are quite distinctive. In OUM.TSK2, the premaxilla extends proportionately further dorso-posteriorly, almost separating the nasals, while its suture with the nasals is smooth-edge, not interdigitating as in the *Dicynodon* specimens (Text-fig. 1C). King (1991) found this to be a consistent and functionally important feature in *Lystrosaurus*.

## DISCUSSION

### *Transitional* Lystrosaurus *from other regions*

Although it is currently agreed that the presence of *Lystrosaurus* indicates lowermost Triassic age (e.g. Cosgriff *et al.* 1982; Olson 1989), the fossil has been reported previously to be found in association with typical members of Upper Permian faunas. Hotton (1967) described a section of the *Lystrosaurus* Assemblage Zone at Lootsberg Pass, Orange Free State, South Africa in which he noted that specimens of *Lystrosaurus* overlapped in the section for about 60 m (200 feet) with typical members of the underlying *Dicynodon* Assemblage Zone fauna such as *Daptocephalus* ( = *Dicynodon*) and *Moschorhinus*. Because the latter were found in differently coloured shales from those containing *Lystrosaurus*, Hotton postulated that two different contemporaneous facies were present, and that *Moschorhinus* and *Daptocephalus* were conservative *Dicynodon* Assemblage Zone forms which had survived into the *Lystrosaurus* Assemblage Zone, perhaps in different niches from those occupied by *Lystrosaurus*.

Kitching (1977) mentioned that in areas with some geographical relief, *Daptocephalus* has often been recorded from the *Lystrosaurus* Assemblage Zone. This has been in situations where the *Lystrosaurus* Assemblage Zone fauna accompanying it could not have been washed or rolled down from higher strata. Similarly, *Lystrosaurus* has also been recorded from the *Dicynodon* Assemblage Zone. Kitching, however, considered such occurrences to represent the circumstance of *Lystrosaurus*

Assemblage Zone sediments having been laid down in previously existing erosional channels of the underlying *Dicynodon* Assemblage Zone rocks, notably in the Lootsberg area. Kitching did not consider this association to represent true contemporaneity of the faunas.

However, contemporaneous faunas do appear to be present in the Upper Permian of China. Olson (1989) noted that mixed *Dicynodon–Lystrosaurus* faunas had been reported from the Guodikeng Formation of Xinjiang, China; and these reports have subsequently been discussed in more detail by Cheng (1993). The earliest Triassic Jiucaiyuan Formation contains specimens of a large species of *Lystrosaurus*, whereas the lower and middle zones of the Late Permian Guodikeng Formation contain the typical Permian anomodont *Striodon.* The Upper Guodikeng Formation, however, contains a small species of *Lystrosaurus* and the typical Permian anomodont *Jimusuaria.* Cheng considered the Upper Guodikeng Formation to contain a transitional, continuous Late Permian–Early Triassic fauna. The pollen assemblage from the Upper Guodikeng is also of a transitional nature.

This situation seems to be very similar to that of the Late Permian Madumabisa Mudstones in Zambia. Cheng (1993) stressed the significance of the discovery of the transitional zone in China with respect to Permo–Triassic stratigraphy and evolution. The Zambian strata are potentially even more important because of the wealth of extremely well-preserved vertebrate fossils they contain. However, an alternative explanation may be that both the Madumabisa Mudstones and the Upper Guodikeng strata are Upper Permian rather than transitional, as evinced by the presence of *Striodon* and *Jimusuaria* in the Chinese localities, and the similarity of the Zambian *Lystrosaurus* specimen to *Dicynodon trigonocephalus.*

### *Stratigraphical use of* Lystrosaurus

The occurrence of *Lystrosaurus* in Late Permian rocks indicates that isolated specimens of the genus should no longer be used for biostratigraphical purposes. Unless other Triassic genera were to be found with the Late Permian ones, it remains reasonable to use an assemblage of genera, of which *Lystrosaurus* is part, to correlate lowermost Triassic rocks, but use of *Lystrosaurus* alone could be misleading. This is obviously unfortunate, since *Lystrosaurus* is the most common genus in many assemblages and so most likely to be encountered in the course of stratigraphical work.

### *Survivorship of* Lystrosaurus *and the end-Permian extinction event*

No other Permian anomodont is known to cross the Permo-Triassic boundary, so why did *Lystrosaurus* survive the end-Permian event when so many other genera did not?

One possibility is that *Lystrosaurus* was adapted to feeding on some component of the transitional flora which succeeded the *Glossopteris* flora of the southern hemisphere towards the end of the Permian (Tucker and Benton 1982). If the food-plant utilized by *Lystrosaurus* became common in the *Dicroidium* flora of the Late Permian–Early Triassic, this could explain the rise in abundance of *Lystrosaurus.* In favour of this, at least as a partial explanation, is the change in organization of the feeding system seen in *Lystrosaurus.* Whereas in many Permian dicynodonts (e.g. *Diictodon, Oudenodon, Robertia*) the backward-pulling component of the external adductor muscles was very substantial and produced longitudinal movement of the lower jaw, in *Lystrosaurus* this component was reduced (King 1990*b*; Cox 1991; King and Cluver 1991). The external adductor muscles had a greater vertical component in the latter and so produced a more strictly orthal jaw movement. King and Cluver (1991) have argued that *Lystrosaurus* was adapted to feeding on resistant vegetation, and had specializations of the skull to deal with this. It is impossible to ascertain which component(s) of the transitional or *Dicroidium* floras might have been the relevant food source.

Further support for this argument is provided by the observation that the Mesophytic flora containing *Dicroidium* replaced the *Glossopteris*-dominated Palaeophytic flora in a north–south sequence through South Africa during the Late Permian to Early Triassic (Andrews 1961). This appears to have coincided with the extinction of numerous anomodont genera and also the migration of *Lystrosaurus* from northern Zambia to South Africa. Although the origin of the Mesophytic flora has been traced to the Late Carboniferous (DiMichele and Aronson 1992; Erwin 1993) with the transition beginning at low latitudes and spreading towards the poles, the final transition did not occur until the Early Triassic. This suggests that *Lystrosaurus* utilized some components of the new Mesophytic flora, either as a specialist or a generalist, in contrast to other anomodont genera which presumably could not feed on the 'new' plant types.

The occurrence of *Lystrosaurus* in the Lower Triassic and not in the Upper Permian has been one of the most clearly visible pieces of evidence for a terrestrial mass extinction event at the Permian-Triassic boundary. However, if *Lystrosaurus* was present in the Late Permian, both the taxonomic extent and the suddenness of the extinction event are brought into question.

The disappearance of so many Permian genera from the fossil record prior to the end of the period is usually interpreted as a consequence of some rapid and drastic environmental change. Smith's (Smith 1990; Smith *et al.* 1993) reviews of Permo-Triassic palaeoenvironments illustrate the increasing aridity of the Southern African area occurring in a north to south direction through the later half of the Permian and into the Triassic. The changes occurred as a result of the northward movement of Africa. The Teekloof Formation of South Africa, deposited contemporaneously with the Madumabisa Mudstones, shows a palaeoenvironment that is already semi-arid with highly seasonal rainfall (Smith *et al.* 1993).

Hotton (1986) noted that striae on the medial wear facet of a tusk in a specimen of *Lystrosaurus* from the Karoo are partly obliterated by polishing. He suggested that this might have been caused by a change in the nature of its food in association with altered feeding circumstances. He postulated the seasonal alternation of harsh and succulent plant material, or alternatively subsurface and above-ground plant elements as an influencing factor. These findings might also suggest that increasing aridity and seasonality of rainfall, accompanied by a major floristic change, had a significant deleterious effect on Late Permian anomodonts, except for *Lystrosaurus* which appears to have been capable of existing in such environments. Erwin's (1994) suggestion of global warming from oceanic anoxia via increased atmospheric carbon dioxide also lends some support to a model of increasing environmental harshness in southern Gondwana. However, the implication from these observations is that the environmental changes occurred gradually. Vacant niches in the changing environment after the event are assumed to have been filled by new radiations centred on surviving taxa. *Lystrosaurus* had previously been interpreted as having evolved as part of a post-extinction radiation, thus constituting part of the evidence for turnover at the Permian-Triassic boundary. However, the presence of *Lystrosaurus* in the Upper Permian of Zambia indicates that it was not part of any new adaptive radiation. This may be true of other members of the *Lystrosaurus* Assemblage Zone fauna, but none have yet been detected in the Permian. If others did exist in the Permian, the evidence for a rapid and taxonomically widespread terrestrial Permian extinction would be reduced. King (1990*a*) has already questioned the suddenness of the event in the Karoo Basin, as there is evidence that several groups of tetrapods were declining in diversity before the end of the Permian. The existence of a supposed post-extinction genus before the event throws more doubt on its nature.

### *Geographical origin of* Lystrosaurus

In 1977, Kitching (p. 23) commented that 'The sudden appearance of this new form of anomodont, *Lystrosaurus*, and its abundance throughout the zone is more indicative of an immigrant form than of one evolved from a branch of the anomodonts from the lower zones. Had the genus *Lystrosaurus* been evolving from a dicynodont from the lower zones then it is considered that corroborative evidence should have been found among some of the large variety of *Cistecephalus* and *Daptocephalus* Zone dicynodonts'. He therefore considered that the origin of *Lystrosaurus* in the Karoo Basin must have been by immigration since there is no evidence from the underlying strata that this dicynodont evolved *in situ*. This is not the case with the Permian strata in Zambia. Not only is *Lystrosaurus* now known from the Upper Permian, but there are also other dicynodont genera which resemble it, in particular *Dicynodon trigonocephalus*. In describing this Zambian form, King (1981) mentioned that it had certain features reminiscent of *Lystrosaurus*, such as the medium-sized skull with subequal length and breadth giving a squarish dorsal profile; very short intertemporal region; short and deep basicranial region; and wide interorbital distance. Several Zambian skulls with this morphology are present in the OUM.TSK collection. These characters suggest that this species of *Dicynodon* is the sister-taxon of *Lystrosaurus* and could imply that *Lystrosaurus* did evolve *in situ* in the Zambian Basin in the Late Permian and migrated into the Karoo Basin subsequently. This underlines the effect that migrations may have upon the observed pattern of faunal change in a discrete area.

An alternative possibility pointed out by A. R. Milner (pers. comm.) is that since the Madumabisa Mudstones are younger than the *Dicynodon* Assemblage Zone and older than the *Lystrosaurus* Assemblage Zone, they could belong with the interregnum between these two zones. Thus, *Lystrosaurus* may have evolved within this interregnum in South Africa, its sudden appearance resulting from the magnitude of the temporal interval in the fossil record, this disunion being partly filled by the Madumabisa Mudstones in Zambia.

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G. M. KING

Faculty of Classics
University of Cambridge
Sidgwick Avenue
Cambridge CB3 9DA, UK
formerly
Division of Earth Sciences
South African Museum
PO Box 61, Cape Town 8000
South Africa

I. JENKINS

Department of Earth Sciences
University of Cambridge
Downing Street
Cambridge CB2 3EQ, UK

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