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A Middle Triassic dicynodont from Germany and the biochronology of Triassic dicynodonts

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With 8 Figures and 1 Table

Summary

We describe a left humerus of a dicynodont from the lower Lettenkeuper of Germany. This specimen cannot be assigned with certainty to any known Triassic dicynodont taxon, and we identify it as aff. *Dinodontosaurus* sp. The only other European Triassic dicynodont, a left humerus from the Muschelkalk of France identified by Broili as cf. *Placerias*, is re-identified as aff. *Parakannemeyeria* sp. Most Triassic dicynodonts had a broad distribution across Pangaea and have an abundant fossil record. We organize this record to identify five, temporally-successive Triassic dicynodont biochrons: *Lystrosaurus* biochron (early Induan), *Kannemeyeria* biochron (late Olenekian−early Anisian), *Shansiodon* biochron (early Anisian), *Dinodontosaurus* biochron (Ladinian) and *Placerias* biochron (late Carnian).

Zusammenfassung

Aus dem unteren Lettenkeuper von Deutschland wird der linke Humerus eines Dicynodontiers beschrieben. Dieser Fund kann keinem bekannten Taxon von Trias-Dicynodontiern sicher zugeordnet werden; er wird als aff. *Dinodontosaurus* bestimmt. Der einzige weitere Trias-Dicynodontier, ein linker Humerus aus dem Muschelkalk von Frankreich, von Broili als cf. *Placerias* bestimmt, gehört zu aff. *Parakannemeyeria*. Die meisten Trias-Dicynodontier waren über Pangäa weit verbreitet und sind fossil gut dokumentiert. Aufgrund ihres Vorkommens können fünf zeitlich aufeinanderfolgende Dicynodontier-Biozonen unterschieden werden: Eine *Lystrosaurus*-Biozone (frühes Induan), eine *Kannemeyeria*-Biozone (spätes Olenek−frühes Anis), eine *Shansiodon*-Biozone (frühes Anis), eine *Dinodontosaurus*-Biozone (Ladin) und eine *Placerias*-Biozone (spätes Karn).

Contents

1. Introduction

Dicynodonts were a widespread group of terrestrial, herbivorous synapsids during the Permian and Triassic (KING 1988, 1990). In Triassic nonmarine strata, they are known from all the continents and are particularly abundant (often the dominant) tetrapod fossils at Early and Middle Triassic localities. The largest nonmarine Triassic stratigraphic terrane that virtually lacks dicynodonts is western Europe. Indeed, there is only one record of a Triassic dicynodont from Europe, a humerus identified as cf. *Placerias* from marine strata of the Muschelkalk south of Avricourt in Lorraine, France (BROILI 1921). This fossil was housed in the collection of the Bayerische Staatssammlung fur Paläontologie und historische Geologie in Munich and destroyed during the Second World War.

Here, we put on record the second Triassic dicynodont discovered in western Europe, a left humerus from the lower Lettenkeuper of Germany. We also discuss briefly the biochronology of Triassic dicynodonts.

2. Locality and Stratigraphic Context

Mr. TRAUGOTT HAUBOLD of Ansbach, a private collector and honorary assistant of the SMNS, collected the dicynodont fossil described here. He discovered it in the Upper Muschelkalk quarry of the firm SCHÖN & HIPPELEIN in Neidenfels in the spring of 1991. The small village of Neidenfels is in the vicinity of Crailsheim, a famous fossil-collecting area of Middle Triassic age (Upper Muschelkalk) in northern Baden-Württemberg, southwestern Germany (Fig. 1). Because of its recognition by the junior author (RW) as an extremely rare dicynodont humerus, Mr. HAUBOLD immediately donated the bone to the Staatliches Museum für Naturkunde in Stuttgart (SMNS). He had discovered it by splitting a sandy marly concretion at the base of the Vitriolschiefer, a series of black, laminated marly clays that immediately overlies the fossiliferous Grenzbonebed of the Upper Muschelkalk (Fig. 2). As a skilled technician, Mr. HAUBOLD prepared the bone by means of a vibro-engraving needle.

The age of the top of the Grenzbonebed and the base of the Vitriolschiefer (Fig. 2), which is the boundary of the Upper Muschelkalk and Lettenkeuper, is Early Ladinian (lowermost Longobard: VISSCHER et al. 1993) or Early/Middle Ladinian (upper Fassan: HAGDORN & GLUCHOWSKI 1993). The transition from the Grenzbonebed to the Vitriolschiefer was a time of regression of the epicontinental Muschelkalk sea in southwestern Germany. In the Grenzbonebed, sedimentation was reduced to a condensed vertebrate detritus layer containing redeposited intraclasts. This facies continues into the lowermost Vitriolschiefer-layer, but did not build a bonebed. Freshwater and terrigenous influences increased throughout the Grenzbonebed deposition and became dominant in the Vitriolschiefer, as is demonstrated by the stratigraphic distribution of marine, brackish and terrestrial vertebrate faunal elements (HAGDORN & REIFF 1988) in the Grenzbonebed. Vertebrate remains are rare in the Vitriolschiefer because they are dispersed horizontally and vertically due to increased rates of sedimentation of clays at the onset of Lettenkeuper deposition.

Fig. 1. Geographic position of the discovery locality of the dicynodont humerus of aff. *Dinodontosaurus* in western Europe (above) and in southwestern Germany (below). Abbreviations are: A = Austria, C = Crailsheim, D = Germany, F = France, N = Neidenfels, S = Stuttgart, SH = Schwäbisch Hall.

As shown by BRUNNER (1973), coarser-grained portions of the Lettenkeuper were transported from the southeast to the northwest, originating on the edge of the Vindelician highland. Amphibian and terrestrial reptile fossils also were transported in this direction. We thus conclude that the biotope of the dicynodont from the basal Vitriolschiefer, here identified as aff. *Dinodontosaurus* sp., was the emerging Vindelician highland located about 70 km southeast of the fossil locality.
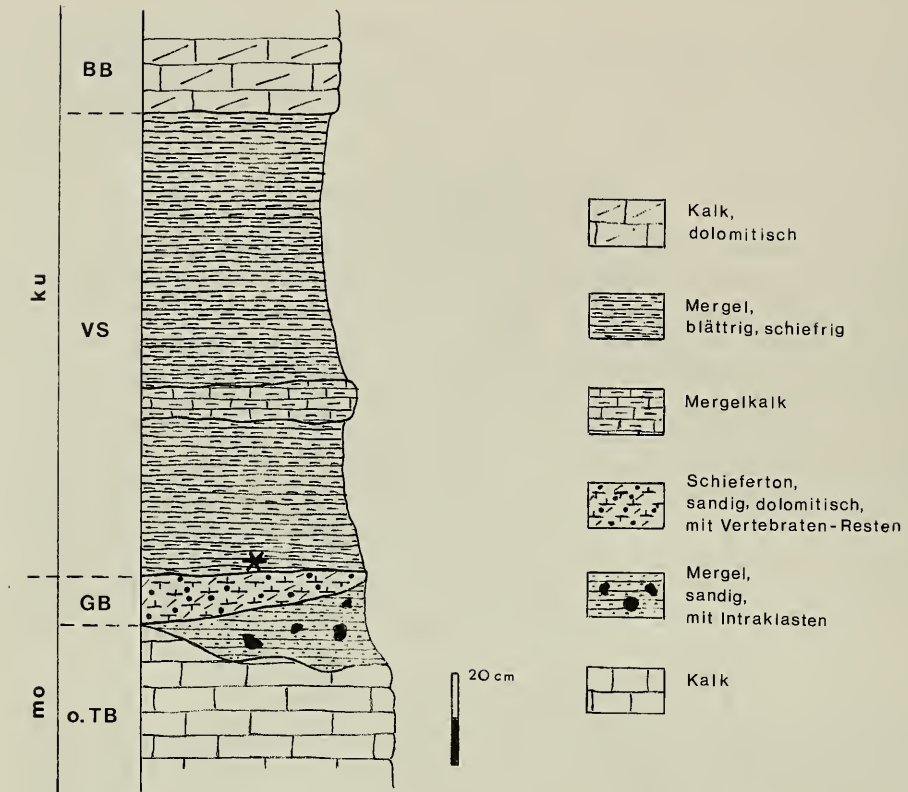
Fig. 2.   Stratigraphic section of the transition from the Upper Muschelkalk (mo) to the
Lower Lettenkeuper (ku) in the quarry of SCHÖN & HIPPELEIN in Neidenfels near
Crailsheim (modified from a section measured by T. HAUBOLD, who discovered the
humerus identified as aff. *Dinodontosaurus* sp.). Abbreviations are: BB = Blaubank,
GB = Grenzbonebed, o.TB = obere Terebratelbank, VS = Vitriolschiefer, * = stra-
tigraphic position of humerus of aff. *Dinodontosaurus*.

3. Description

The dicynodont left humerus (Figs. 3−5) is SMNS 56891. It is a short, robust bone
with considerably expanded proximal and distal ends that are twisted about the shaft
(the angle subtended by this twisting is approximately 60 degrees: Table 1). The pro-
ximal articular surface is a broad convex edge which has a slightly rugose surface.
This surface has a tall, triangular cross section in proximal view, with the most acute
angle of the triangle pointing anteriorly.

The proximal articular surface protrudes anteriorly to become confluent with the
deltopectoral crest. This crest is 53% of the maximum proximo-distal length of the
entire humerus and is a thick flange of bone with a knobby antero-distal half of its
anterior edge. Four distinct, knob-like tuberosities are present, one of which (the
postero-dorsal one) is broken. Away from the tuberosities, the anterior edge of the
deltopectoral crest has a roughened surface. The deltopectoral crest and head of the
humerus occupy its proximal half, which is slightly convex dorsally and slightly con-
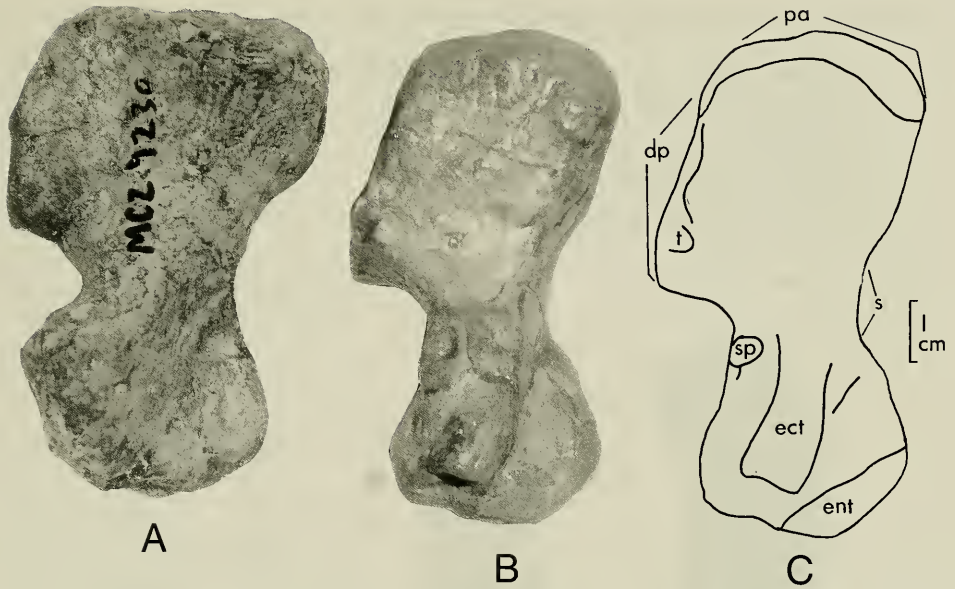cave ventrally.

Fig. 3. Dorsal views of dicynodont left humeri. A: *Dinodontosaurus tener*, MCZ 9230. B−C: SMNS 56891. − Abbreviations are: dp − deltopectoral crest, ect − ectepicondyle, ent − entepicondyle, pa − proximal articular surface, s − shaft, sp − supinator process, t − tuberosity.

Fig. 4. Ventral views of dicynodont left humeri. A: *Dinodontosaurus tener*, MCZ 9230. B−C: SMNS 56891. − Abbreviations are the same as in Fig. 1.

Tab. 1.   Measurements (in mm) of SMNS 56891 and MCZ 9230.

Measurement	SMNS 56891	MCZ 9230
proximo-distal length	79.1	68.3
proximal width	34.7	40.7
distal width	42.8	42.7
length deltopectoral crest	41.9	33.5
maximum width shaft	24.4	21.9
angle twist of heads (degrees)	± 60	± 40

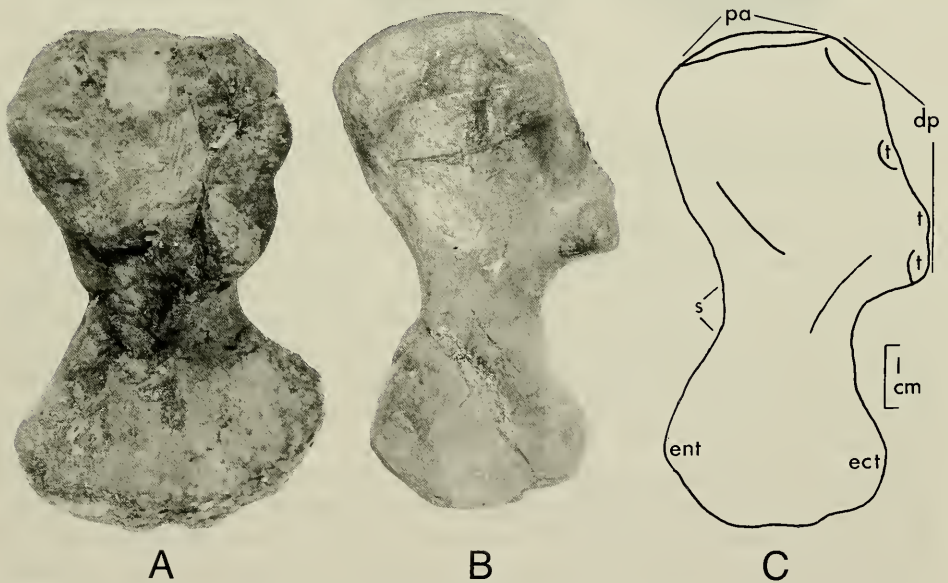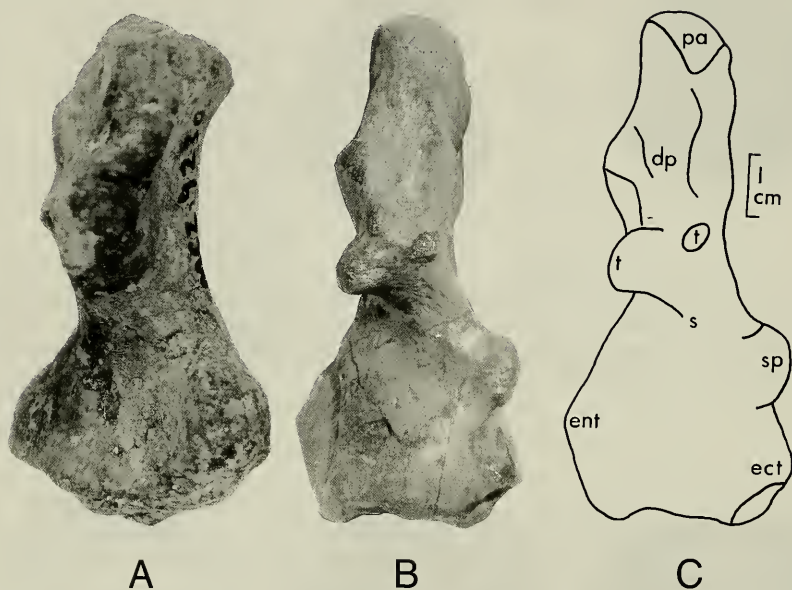

Fig. 5.   Anterior views of dicynodont left humeri. A: *Dinodontosaurus tener*, MCZ 9230. B–C: SMNS 56891. – Abbreviations are the same as in Fig. 1.

The shaft distal to the deltopectoral crest is very short and stout, though very constricted relative to the proximal and distal ends of the bone. Its cross section is a somewhat angular oval. The distal end of the humerus flares out to form two flanges of bone. The larger flange is the entepicondyle, which forms a nearly flat, plate-like projection posteriorly. The attachment point for the flexor muscles of the forearm on the postero-distal edge of the entepicondyle is a blunt, slightly convex surface. No entepicondylar foramen is present. A compression fracture has slightly displaced the entepicondyle dorsally.

This fracture somewhat exaggerates the dorsal concavity and ventral convexity of the distal end of the humerus that separates the entepicondyle from the ectepicondyle. Viewed distally, the ectepicondyle has an almost cylindrical cross section that expands in diameter distally. The antero-distal edge of the ectepicondyle is a circular pit with a rim of raised bone that becomes a distally oriented flange on the postero-dorsal edge of the pit. Anterior and proximal to the ectepicondyle is a blunt, anteriorly-directed supinator process. The anterior edge of this process is a convex, roughened surface that is flattened in a dorso-ventral plane.
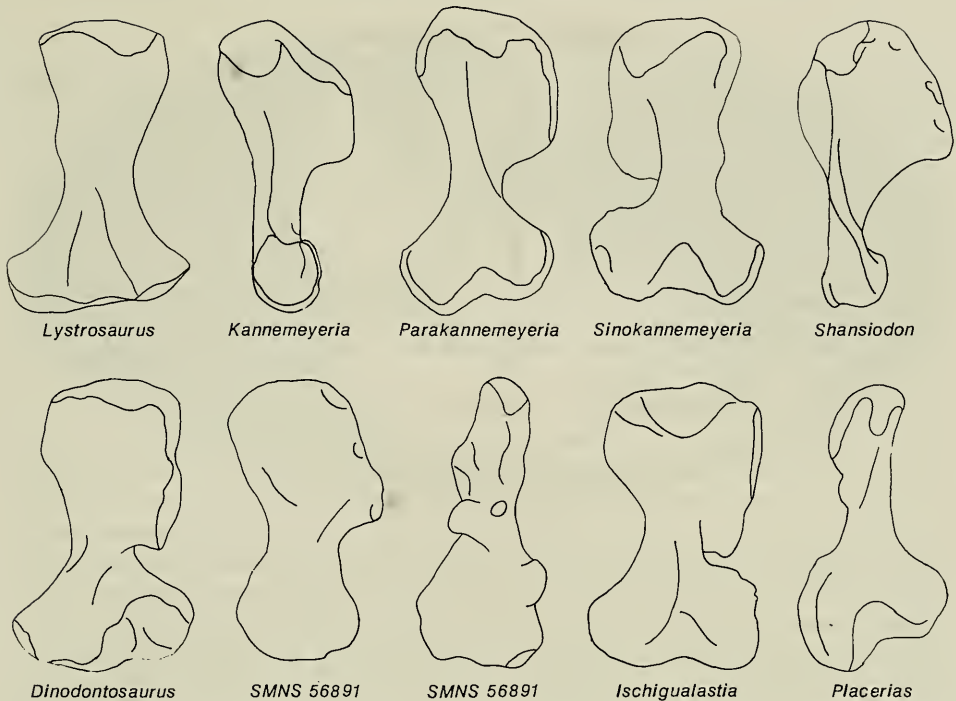
Fig. 6. Dorsal views of humeri of selected Triassic dicynodonts (except for *Kannemeyeria*, second view of SMNS 56891 and *Placerias*, which are anterior views). All humeri are drawn to the same size, so not to scale (drawings after CAMP & WELLES 1956; SUN 1963; DEFAUW 1986).

4. Identification

Dicynodont taxonomy is based almost totally on cranial characters, so precise identification of isolated postcranial elements such as SMNS 56891 is nearly impossible. DEFAUW (1986), in an initial study of postcranial variation among dicynodonts, noted significant differences among their postcrania but did not attempt to differentiate dicynodont taxa on this basis. Clearly, such a basis exists (see, for example, Fig. 6), and it needs to be developed in the future.

SMNS 56891 does not correspond in morphology to any known Triassic dicynodont (Fig. 6). Measurements (Table 1) indicate it is about the same size as MCZ (Museum of Comparative Zoology, Harvard University, Cambridge) 9230, a left humerus of *Dinodontosaurus tener* from the Santa Maria Formation of Rio Grande do Sul, Brazil. However, significant differences exist between SMNS 56891 and *D. tener*, including: (1) the humerus of *D. tener* is more robust, with a much broader deltopectoral crest, shorter and wider shaft and relatively broader distal end; (2) the *D. tener* humerus lacks a supinator process; and (3) the anterior face of the distal end of the humerus of *D. tener* lacks the pronounced dorsal concavity and ventral convexity of SMNS 56891. Clearly, SMNS 56891 does not belong to *Dinodontosaurus* (Figs. 3–6), nor can it be readily assigned to any other Triassic dicynodont taxon. Because its greatest resemblance is to *Dinodontosaurus* among the Triassic dicynodonts, we identify SMNS 56891 as aff. *Dinodontosaurus* sp.

5. BROILI's Dicynodont

BROILI (1921) described and illustrated a dicynodont humerus from the Upper Muschelkalk of Lorraine as cf. *Placerias*. The bone was never freed from the rock, so only part of its dorsal aspect could be examined and, as mentioned above, it was lost during the Second World War. CAMP & WELLES (1956: 256) concluded that this specimen does not represent *Placerias* and probably pertains to a Middle Triassic dicynodont such as *Sinokannemeyeria*. They noted:

It [BROILI's specimen] is about half the length of *Placerias* and is flat and thin. The distal and proximal ends lie in the same plane rather than at right angles to each other . . . Broili's specimen is smooth with fine striae on its surface. The shape and extent of the expanded deltoid crest indicate that it is the left humerus of an anomodont, though not *Placerias*. It more nearly resembles *Sinokannemeyeria*.

Nevertheless, KING (1988: 108, 160) listed *Placerias* from Europe based on BROILI's (1921) report.

The left humerus (BROILI misidentified it as a right humerus) illustrated by BROILI (1921, fig. 1) is about twice the size of SMNS 56891. According to BROILI (1921), its maximum length is 170 mm and greatest width across the deltopectoral crest is 90 mm. BROILI did not prepare the humerus out of the rock, so he illustrated it only in anterior view with much of the distal end still encased in rock. In addition to the size difference (which, of course, could be due to ontogenetic differences), other significant differences between BROILI's (1921) specimen and SMNS 56891 include: (1) BROILI's specimen has a much shorter deltopectoral crest proximo-distally; (2) BROILI's specimen has a relatively longer and much narrower shaft; and (3) no supinator crest is present on BROILI's specimen. BROILI's specimen resembles *Kannemeyeria*, *Sinokannemeyeria* and *Parakannemeyeria* more than it does SMNS 56891. In size, it is only slightly smaller than a juvenile specimen of *Parakannemeyeria youngi* illustrated by SUN (1963, fig. 42). However, assignment of BROILI's specimen to either *Kannemeyeria*, *Parakannemeyeria*, or *Sinokannemeyeria* is impossible simply because of a lack of additional information on the dorsal and distal morphology of BROILI's specimen.

Nevertheless, two things seem certain about BROILI's specimen. First, it is not the same taxon as SMNS 56891. Second, it is not *Placerias*, so its identification as cf. *Placerias* was misleading. We identify it as aff. *Parakannemeyeria* sp.

6. Triassic Dicynodont Biochronology

6.1. Introduction

Dicynodonts had a Pangaea-wide distribution during most of the Triassic (Fig. 7), so they have great potential for correlating Triassic nonmarine strata. Here, we briefly review Triassic dicynodont biochronology, in part to establish better the biochronological significance of SMNS 56891. In so doing, we modify the dicynodont zonation of COOPER (1982) (Fig. 8) and also differ in some taxonomy and correlations from recent dicynodont-based biochronology proposed by COX (1991) and BATTAIL (1993).

6.2. *Lystrosaurus* biochron

Lystrosaurus has a nearly Pangaea-wide distribution in early Induan strata, being known from South Africa, Antarctica, India, China, Russia and possibly Laos and
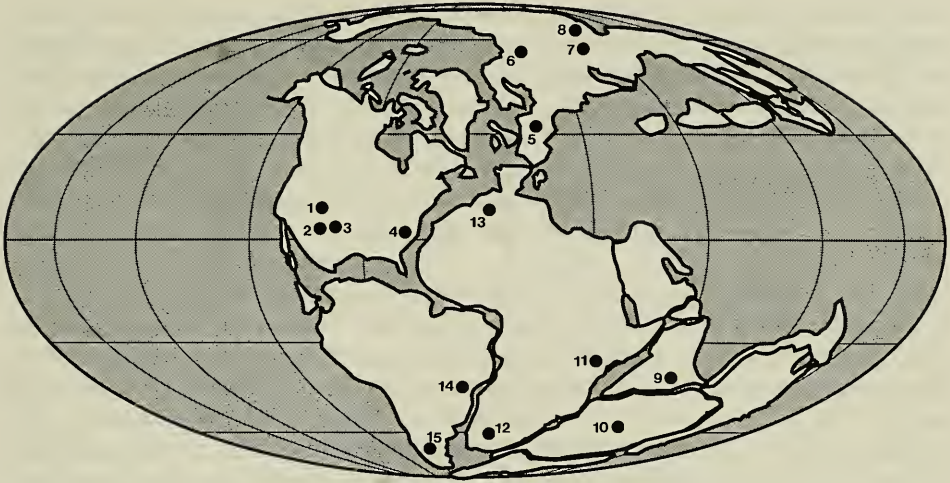
Fig. 7. Map of principal Triassic dicynodont localities. Localities are: 1 — Popo Agie Formation, Chinle Group, Wyoming, USA; 2 — Blue Mesa Member, Petrified Forest Formation, Chinle Group, Arizona, USA; 3 — Los Esteros Member, Santa Rosa Formation, north-central New Mexico; 4 — Pekin Formation, Newark Supergroup, North Carolina, USA; 5 — Muschelkalk and Lettenkeuper, France and Germany; 6 — Cis-Urals, Russia; 7 — Guodikeng Formation, Junggur basin, China; 8 — Ermaying Formation, Ordos basin, China; 9 — Pranhita-Godavari Valley, India; 10 — Fremouw Formation, Antarctica, 11 — Manda Formation, Tanzania ; 12 — Karoo basin, South Africa; 13 — Argana Formation, Morocco; 14 — Santa Maria Formation, Brazil; 15 — Ischichuca Formation, Argentina.

	COOPER		LUCAS & WILD		
TRIASSIC	Norian	*Plateosaurus* Zone		Rhaetian	TRIASSIC
		Placerias Zone		Norian	
	Carnian	*Stahleckeria* Zone	*Placerias* biochron	Carnian	
	Ladinian	*Dinodontosaurus* Zone	*Dinodontosaurus* biochron	Ladinian	
	Anisian	*Tetragonias* Zone		Anisian	
			Shansiodon biochron		
	Scythian	*Kannemeyeria* Zone	*Kannemeyeria* biochron	Olenekian	
PERMIAN	Dorashamian	*Lystrosaurus* Zone		Induan	
	Djulfian		*Lystrosaurus* biochron		

Fig. 8. Our biochronology of Triassic dicynodonts compared to the biostratigraphic scheme of COOPER (1982).

Australia (e.g. Colbert 1974; Cosgriff et al. 1982). Its occurrences define a *Lystrosaurus* biochron previously referred to as the *Lystrosaurus* zone or *Lystrosaurus* beds. We use the term biochron here to refer to the time equivalent to a taxon range zone, instead of the biostratigraphic term zone or the lithostratigraphic term bed, both of which do not necessarily refer to a time interval. The small dicynodont *Myosaurus gracilis* co-occurs with *Lystrosaurus* in South Africa and Antarctica (Hammer & Cosgriff 1981). Cooper (1982) considered the *Lystrosaurus* "Zone" to be of Late Permian age, but we follow recent workers who assign the strata that contain *Lystrosaurus* to the earliest Triassic (Fig. 8).

We note, however, that a problem, unresolvable at present, exists with regard to assigning the *Lystrosaurus* biochron to the Permian, Triassic or Permian-Triassic. Most workers have long assumed that the first appearance datum (FAD) of *Lystrosaurus* corresponds to the base of the Triassic, even though there is no way to correlate this FAD to the base of the marine Triassic of the standard global chronostratigraphic scale (SGCS), which is the base of the Induan = the FAD of the ammonoid *Otoceras* (Tozer, 1984). Furthermore, the FAD of *Lystrosaurus* has long been supposed to postdate the last appearance datum (LAD) of the characteristically Late Permian dicynodont *Dicynodon* (= *Daptocephalus*). However, in the Junggur basin of northwestern China and the Karoo basin of South Africa, fossils of *Dicynodon* and *Lystrosaurus* co-occur in an overlap zone. At Dalonggkou in the Junggur basin, in the upper part of the Guodikeng Formation, they co-occur over a 30 m thick interval of mostly purplish red silty mudstone (Cheng & Lucas 1993). In South Africa, *Dicynodon* and *Lystrosaurus* overlap in a 15 m thick interval at the base of the Palingkoof Member of the Balfour Formation (Smith 1993). No biostratigraphic data available from either the Chinese or South African sections provides a convincing correlation to the SGCS, but evidence from Russia and Greenland indicates that at least some (though not necessarily all) *Lystrosaurus* fossils are of Triassic age. In Russia, *Lystrosaurus* co-occurs with the amphibians *Luzocephalus* and *Tupilakosaurus* (Ochev & Shishkin 1989). These amphibians also are known from marine strata with Induan ammonoids in Greenland (Ochev & Shishkin 1989). This is the most direct evidence that part of the *Lystrosaurus* biochron is Triassic, but whether or not the FAD of *Lystrosaurus* is the base of the Triassic still needs to be determined.

6.3. *Kannemeyeria* biochron

Kannemeyeria has a distribution in deposits that straddle the Early-Middle Triassic boundary that is nearly as broad as that of *Lystrosaurus*. Its fossils are known from Argentina, South Africa, South West Africa, Zambia, Russia, China and India.

Kannemeyeria is a medium- to large-sized dicynodont in which both sexes have tusks. In dorsal view, the zygomatic arches are parallel or nearly so. The high and narrow parietal crest is at a steep angle to the frontal portion of the skull and does not expose the interparietal dorsally. The orbit is relatively large, and the pre-canine region of the snout is relatively short. There is a mid-nasal ridge, and the premaxilla is drawn out into a pointed snout. The type species of *Kannemeyeria* is *K. simocephalus* (Weithofer 1888) from South West Africa. Only one other species is valid, *K. cristarhynchus* Keyser & Cruickshank 1979 (= *K. argentinensis* Bonaparte 1966).

Critical to recognition of the *Kannemeyeria* biochron is the synonymy of *Rechnisaurus*, *Uralokannemeyeria* and *Shaanbeikannemeyeria* with *Kannemeyeria*. COX (1991) has synonymized *Uralokannemeyeria* and *Shaanbeikannemeyeria* with *Rechnisaurus*, and we agree fully with this decision. However, COX (1991) as well as KING (1988), BANDYOPADHYAY (1989) and DEFAUW (1993) have retained *Rechnisaurus* as a genus distinct from *Kannemeyeria*. The principal character that can be marshalled to distinguish *Rechnisaurus* from *Kannemeyeria* is the former's possession of a blunt snout. Like KEYSER & CRUICKSHANK (1979), we regard this as a species level difference between *K. cristarhynchus* and *K. simocephalus*.

Kannemeyeria biochron localities are: (1) Yerrapalli Formation, Pranhita-Godavari Valley, India; (2) lower Omingonde Formation (Etjo Beds), Etjo Mountain, South West Africa; (3) upper Burgersdorp Formation, South Africa; (4) lower fossiliferous horizon of N'tawere Formation, Luangwa Valley, Zambia; (5) upper Puesto Viejo Formation, Mendoza Province, Argentina; (6) lower Ermaying Formation, Ordos basin, China; and (7) Donguz Svita, Orenburg District, Russia. These occurrences are either of late Early Triassic (late Olenekian) or of earliest Middle Triassic (early Anisian) age (BANDYOPADHAY 1988).

6.4. *Shansiodon* biochron

LUCAS (1993a) established the *Shansiodon* biochron for the distribution of this small- to medium-sized dicynodont. Its occurrences are: (1) Ermaying Formation, Ordos basin, China; (2) Donguz Svita, Orenburg District, Russia; (3) Manda Formation, Tanzania; (4) Omingonde Formation, South Africa; (5) N'tawere Formation, Zambia; and (6) Cerro de las Cabras Formation, Mendoza Province, Argentina. All of these occurrences are of earliest Middle Triassic (early Anisian) age. There thus is overlap of the *Kannemeyeria* and *Shansiodon* biochrons during the early Anisian, as COOPER (1980) noted.

COOPER (1982) identified a *Tetragonias* "Zone" (we consider *Tetragonias* to be a junior synonym of *Shansiodon*: LUCAS 1993a) which also included occurrences of *Kannemeyeria* younger than his *Kannemeyeria* "Zone" (Fig. 8). We prefer instead to indicate the clear temporal overlap of *Kannemeyeria* and *Shansiodon* in our biochronological scheme (Fig. 8).

In China, the so-called "*Sinokannemeyeria* fauna" or "kannemeyeriid fauna" includes *Shansiodon* (e.g. SUN 1972; CHENG 1981). The Chinese endemic dicynodonts *Sinokannemeyeria* and *Parakannemeyeria* are thus of *Shansiodon*-biochron age, except for the earliest record of *Parakannemeyeria*, which is in *Kannemeyeria*-biochron-age strata of the lower Ermaying Formation of the Ordos basin (CHENG 1981; LUCAS 1993c).

6.5 *Dinodontosaurus* biochron

A dearth of late Middle Triassic (Ladinian) nonmarine tetrapod faunas exists, the main ones being from South America. *Stahleckeria potens* (= *Barysoma lenzii*: LUCAS 1993b) and *Dinodontosaurus* have been listed as Late Triassic dicynodonts from the Santa Maria Formation of Rio Grande do Sul, Brazil (KING 1988, 1990), but they are of Middle Triassic age (BARBARENA 1977; BARBARENA et al. 1985; LUCAS 1993b).

Dinodontosaurus occurs in the Santa Maria Formation of Brazil and the Ischichuca (Chañares) Formation of Argentina (Cox 1965, 1968), strata generally considered to be of Ladinian age. Because of its restriction to South America, correlation of the *Dinodontosaurus* biochron across Pangaea is problematic. Both German dicynodonts — the specimen described by Broili and SMNS 56891 — are from strata that can be stratigraphically compared with strata of *Dinodontosaurus*-biochron age. Neither specimen is *Dinodontosaurus*, but both most resemble Middle Triassic dicynodonts: Broili's is most similar to a juvenile *Parakannemeyeria* and SMNS 56891 most resembles *Dinodontosaurus*. The unique morphology of both German humeri may indicate they are hitherto unknown taxa and thus represent an unknown and endemic Middle Triassic dicynodont fauna in Europe. Difficulty in correlating the *Dinodontosaurus* biochron in part may reflect a Ladinian period of tetrapod endemism and also reflects the dearth of Ladinian faunas.

Stahleckeria is the largest dicynodont of the *Dinodontosaurus* biochron (indeed, it is the largest dicynodont), but it is known only from Brazil. The endemism of so large a herbivore on Pangaea suggests endemism of the land-vertebrate fauna of the Ladinian. The best candidate for an occurrence of *Stahleckeria* outside Brazil is *Elephantosaurus* from Russia. Vjushkov (1969) described *Elephantosaurus jachimovitschi* from the Kuyurgazin district of Bashkirskaya, Russia. The strata from which this dicynodont was derived, the Yushatyr Svita, are supposed to be of Middle-Late Triassic age. *E. jachimovitschi* is known solely from a fragment of the interorbital region of the skull (Vjuschkov 1969, fig. 2). It was originally considered to be a kannemeyeriid near *Stahleckeria* with a much thicker skull roof and a distended orbital margin. However, as King (1988) observed, the holotype is so incomplete that *E. jachimovitschi* is best considered a nomen dubium.

Cooper (1982) recognized successive *Dinodontosaurus* and *Stahleckeria* ”Zones“ in his biostratigraphic scheme (Fig. 8). However, we do not accept this simply because *Dinodontosaurus* and *Stahleckeria* co-occur in the Santa Maria Formation of Brazil, which is a correlative of the Ischichuca Formation of Argentina (Lucas 1993b).

6.6. *Placerias* biochron

One of the last dicynodonts, *Placerias*, is known from late Carnian (Tuvalian) strata in the USA (Wyoming, Arizona, North Carolina) and Morocco. Lucas & Hunt (1993) reviewed the North American *Placerias*, recognizing only one species, *P. hesternus* (= *P. gigas*). Cooper's (1982) assignment of the *Placerias* Zone to the Carnian and Norian cannot be supported; *Placerias* is known only from upper Carnian strata.

Three dicynodont taxa have been named from Upper Triassic strata of the Argana Formation in Morocco: *Moghreberia nmachouensis* Dutuit 1980; *Azarifeneria barrati* Dutuit 1989a and *A. robustus* Dutuit 1989b. Dutuit (1980, 1988) based *M. nmachouensis* on two skulls and assorted postcrania. This taxon closely resembles *Placerias*, but supposedly differs cranially in features that include a lower, shorter interparietal crest and convex skull roof above the orbits. Dutuit's (1988) plates indicate that the cranial material of *M. nmachouensis* is much crushed and distorted, so his reconstruction of the skull, which makes it look quite distinct from *Placerias*, is open to reinterpretation. Indeed, Lucas (1990) and Cox (1991) considered

Moghreberia to be a synonym of *Placerias*. We follow this conservative conclusion, and identify the Argana taxon as *Placerias nmachouensis*.

DUTUIT (1989a) based *Azarifeneria barrati* on two skull fragments, part of an interparietal crest and part of the occipital plate, presumably of a single individual. In diagnosing *A. barrati*, DUTUIT only distinguished it from the gigantic Brazilian dicynodont *Stahleckeria potens*. DUTUIT correctly noted that the narrow interparietal crest which includes the postorbitals and the divergent basioccipitals of the holotype of *A. barrati* distinguish it from *S. potens*. But, these are also features that distinguish *Placerias nmachouensis* from *S. potens* (DUTUIT 1988). DUTUIT (1989a) estimated the skull length of the holotype specimen of *A. barrati* as 0.8 m, whereas that of the specimens he described as *P. nmachouensis* is about 0.5 m (DUTUIT 1988). Other than by size, *A. barrati* and *P. nmachouensis* do not differ. Both are from nearby localities and similar stratigraphic horizons. It seems most reasonable to regard *A. barrati* as a junior synonym of *P. nmachouensis*.

DUTUIT (1989b) named a second species of *Azarifeneria*, *A. robustus*, for an incomplete lower jaw from the same locality as the type material of *M. nmachouensis*. As DUTUIT (1989b) noted, this jaw is more massive, deeper and has a shorter symphysis than that of *P. nmachouensis*. However, this incomplete lower jaw cannot be distinguished from that of *Stahleckeria potens* (HUENE 1935, pl. 6, figs. 2–3) or *Placerias hesternus* (CAMP & WELLES 1956, fig. 24). Furthermore, dicynodont jaws of larger individuals of a single taxon tend to be more massive and deeper than those of smaller individuals. So, we are not certain that the holotype of *A. robustus* is not just a jaw fragment of a large individual of *P. nmachouensis*. Indeed, DUTUIT (1988, pl. 2, figs. A-C) originally illustrated the holotype of *A. robustus* as a specimen of *P. nmachouensis*. In light of these observations, we consider *A. robustus* to be a synonym of *P. nmachouensis*. There is thus only one valid taxon of dicynodont from the Upper Triassic of Morocco, *P. nmachouensis* from localities XI and XII of level t. 5 of the Argana Formation.

The only Late Triassic dicynodont reported from Brazil is a skull named *Jachaleria candelariensis* by ARAUJO & GONZAGA (1980) from the Caturrita Formation, which overlies the Santa Maria Formation in Rio Grande do Sul. We cannot, however, differentiate this skull from that of *Ischigualastia* (LUCAS 1993b). Dicynodont taxa from the Upper Triassic of Argentina are *Ischigualastia jenseni* COX 1962 and *Jachaleria colorata* BONAPARTE 1972. Correlation of *Ischigualastia* occurrences in Argentina with other Late Triassic tetrapod faunas outside of South America has always been fraught with problems because of the endemism of the South American faunas. Here, we advocate the correlation of HUNT & LUCAS (1991), LUCAS et al. (1992) and LUCAS & HUNT (1993) that the *Ischigualastia* occurrences are of late Carnian age and approximately correlative with the *Placerias* biochron of this article.

Indeterminate dicynodonts have been reported from the Upper Triassic Maleri Formation in India by KUTTY et al. (1988) and KUTTY & SENGUPTA (1989). These specimens are skull fragments, a partial humerus and an atlantal neural arch (KUTTY & SENGUPTA 1989), but they have not been described or illustrated. The occurrence of the primitive phytosaur *Paleorhinus* in the Maleri Formation indicates the *Paleorhinus* biochron of late Carnian (Tuvalian) age (HUNT & LUCAS 1991a), which overlaps the *Placerias* biochron. It is thus likely that the Maleri Formation dicynodonts are of *Placerias* biochron age.

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