Evolution, ecology and biogeography of the Triassic Reptiles
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# Late Triassic terrestrial vertebrate extinctions: stratigraphic aspects and the record of the Germanic Basin

**Abstract** — A case is made for the reality of the late Carnian extinction event among tetrapods in particular, and for marine and terrestrial animals as a whole. Recent criticisms, particularly that the event is merely an artefact of a poor fossil record, are refuted. Indeed, the late Carnian extinction event appears to have been more significant than the terminal Triassic extinction for terrestrial tetrapods. More documentation is required of the events during the Late Triassic, and this must be founded first on detailed studies of continuous stratigraphic sections that span the time intervals of interest. There are ten or so major successions of this type around the world, and those in the Germanic basin, south-west England, south-western North America, Argentina (?), and India (?) appear to span the Carnian/ Norian boundary, and to yield reasonably abundant tetrapod remains below and above the boundary. The Triassic/ Jurassic boundary is much harder to study because of major facies changes in Europe, gaps in the succession in Argentina and India, poor dating control in south-western North America, south-west England, South Africa, and China, and restricted fossil content below the boundary in eastern North America. The extensive, and well-studied, record of Late Triassic amphibians and reptiles from south-west Germany gives the opportunity of a detailed study of Late Triassic faunal changes, but the record is patchy and results are not as clear as they might be. Nevertheless, the record of sites and fossils is documented in detail for the first time.

## INTRODUCTION

Reptiles and amphibians underwent major turnovers during the Late Triassic. The Middle Triassic faunas of diverse temnospondyls, mammal-like reptiles, thecodontians, prolacertiforms, and rhynchosaurs were replaced, by Early Jurassic times, by a range of new groups, including lissamphibians, turtles, crocodilomorphs, pterosaurs, dinosaurs, lepidosaurs, and mammals. Only a few temnospondyl and mammal-like reptile families survived beyond the Late Triassic.

Earlier authors (e.g. Colbert 1949, 1958) assumed a single extinction event in the Late Triassic, presumably coinciding with the well-known marine mass extinction. However, more detailed study has shown that the terrestrial tetrapod turnover may have taken place well before the end of the Triassic, near the Carnian/ Norian stage boundary, as noted by Bakker (1977), Charig (1979), Benton (1983,1986a, b, 1991a), Olsen and Sues (1986), Parrish (1986, 1989), Lucas (1990), and Dubiel *et al.* (1991).

This view has been criticised by Sepkoski (1986), Olsen *et al.* (1987, 1988, 1991), Sues and Olsen (1990), and Hallam (1990), who regard the key turnover as occurring at the Triassic-Jurassic boundary. The Carnian/ Norian event is seen by these authors as an artefact of poor collecting or as a merely local event. Hallam (1990, p. 580) writes of the postulated end-Carnian mass extinction, «this event is likely to have been regional, not global», implying that, if real, it was merely Alpine in extent. In particular, he argues that the intercalation of the Raibl Formation, a partially nonmarine unit, in the otherwise marine sequence of the Northern Calcareous Alps of Austria creates a break in the record that gives the appearance of an extinction event. The effect of this regressive phase will have to be assessed for the marine record in order to see whether it is sufficient to explain away the Carnian extinction peaks found by many authors (e.g. Benton 1986a; Sepkoski 1986; Sepkoski and Raup 1986; Johnson and Simms 1989; Simms and Ruffell 1989, 1990). Hallam's (1990, p. 580) strong hint that the late Carnian extinction among tetrapods is related to local Alpine phenomena or to gaps in the record is insufficiently demonstrated.

Sues and Olsen (1990, p. 1020) consider that much of the postulated late Carnian extinction among tetrapods is the result of «an apparent temporal discontinuity between the geographically disjunct Middle Triassic synapsid-dominated assemblages of Gondwana and the classic archosaur-dominated communities from the Upper Triassic of Laurasia». On the contrary, most of the late Carnian faunas that I considered (Benton 1986, 1991) are Laurasian (14 from Europe and North America; seven from Gondwana), while the same distribution applies for the early Norian faunas (six from Europe and North America; three from southern Africa) (see Benton 1993 for full documentation).

The view that the late Carnian extinction event is merely local in occurrence, or is the result of poor sampling, has been strongly countered by Simms and Ruffell (1990), Simms *et al.* (1993) and Smith (1990) for the marine realm, and by Benton (1991) for the terrestrial record. These latter authors find that several marine groups (ammonoids, bivalves, bryozoans, conodonts, coral reefs, echinoids, crinoids, and marine tetrapods) show significant global-scale extinction during, or at the end of, the Carnian (Fig. 1). Indeed, Sepkoski's (1990) latest analysis of marine genera confirms the existence of a significant Carnian extinction peak. In addition, his studies of individual taxonomic groups show a major Carnian extinction peak for the corals, bryozoans, bivalves, and echinoderms, an intermediate peak for the foraminifera and vertebrates, and a minor peak for the ammonoids [the terms major, intermediate, and minor, as used here, are defined by Sepkoski 1990, p. 38]. Only the brachiopods, gastropods, and arthropods show no extinction peak in the Carnian.

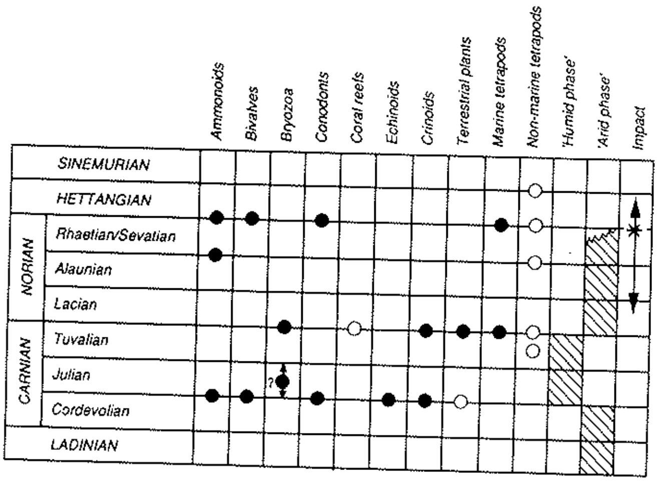


Fig. 1 - Major events in the Late Triassic and earliest Jurassic of various marine and non marine groups. Extinctions are shown by solid circles and times of high turnover by open circles. Palaeontological data are based on Simms and Ruffell (1990) and Benton (1991). Broad climatic phases are noted from Simms and Ruffell (1990), and the range of postulated dates for the Manicouagan impact structure in Canada are taken from Olsen *et al.* (1987). The Manicouagan crater has been redated as 214 MYA, close to the Carnian-Norian boundary (Hodych and Dunning (1992).

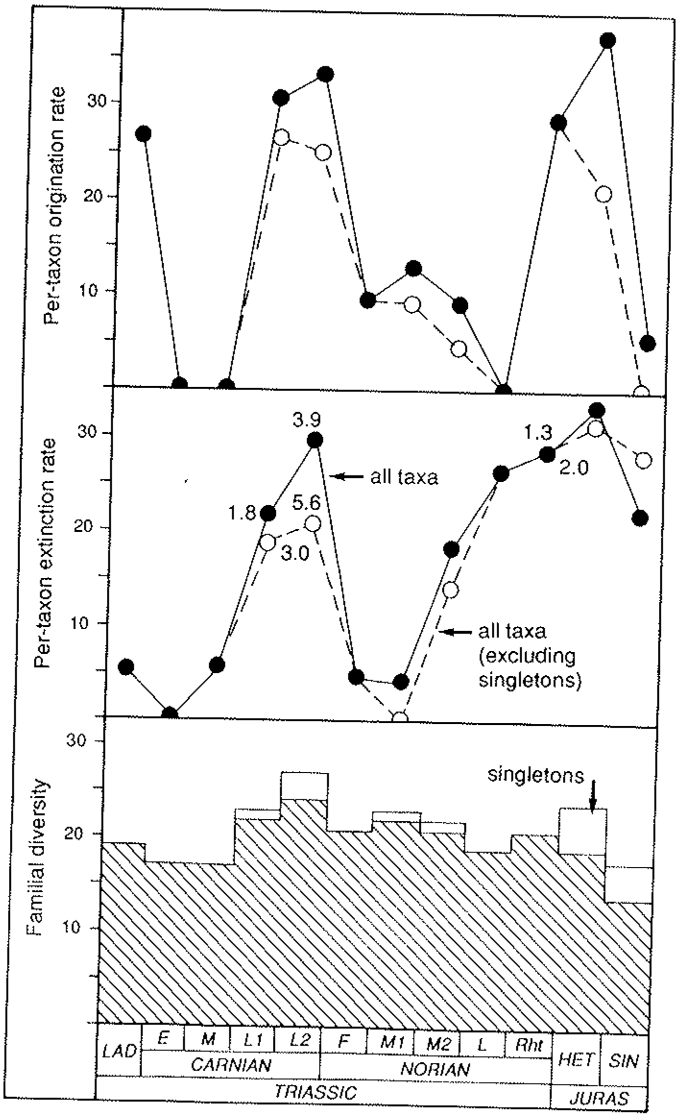


Fig. 2 - Global data on the diversity (a), extinction rates (b), and origination rates (c) of non-marine tetrapods during the Late Triassic and earliest Jurassic. The rates are measured as pertaxon percentages, based on data in Benton (1991); they are not scaled to time, since the durations of the time intervals used cannot be estimated accurately. The rate values are plotted separately for all taxa and for all non-singleton taxa. Mean terminal species diversities of the families dying out are also indicated for the late Carnian, and the Rhaetian, extinction events. Abbreviations: E, Early; HET, Hettangian; JURAS, Jurassic; L, Late; LAD, Ladinian; M, Middle; Rht, Rhaetian; SIN, Sinemurian.

Benton (1991) showed that the late Carnian event was much more significant in mediating tetrapod turnover than was the end-Triassic event. The late Carnian event saw the disappearance of nine species-rich families, while only six species-poor families died out at the end of the Triassic (Fig. 2). In addition, the end-Carnian event cleared the way for the radiation of many major new groups, as noted above (?lissamphibians, turtles, crocodilomorphs, pterosaurs, dinosaurs, lepidosaurs, mammals), while the end-Triassic event was followed by the appearance of four small dinosaur families, two of mammal-like reptiles, and some other 'families' with only one species each.

There are many problems with attempting these kinds of global-scale analyses, problems of correlation and dating in particular, which make it hard to establish patterns of change with precision. It is possible to draw up correlation charts of the major terrestrial vertebrate-bearing formations of the world, but many of the correlations are based on the vertebrates themselves, and hence produce a strong circularity of argument if the faunal lists are compiled for studies of extinction and turnover. In fact, only the Germanic Triassic, and parts of the North American Late Triassic successions are dated by independent means, particularly palynology, although this is not yet a sufficiently powerful technique to allow fine-precision correlation and dating. Other dating techniques, such as magnetostratigraphy and the use of ostracods and fishes, are still in their infancy.

Other major problems concern the ways in which the data are assessed, and the nature of the taxa involved. Family-level taxa are most often used in taxon-counting.

Many of these are established as monophyletic groups, but there is no objective way by which to determine which clades are of family rank (as opposed to ordinal or generic status). Also, of the families involved in calculations of global rates of origination and extinction, all have very different ecological values. Many, for example, are based on single species, or even single specimens, from unique localities, and they cannot be said to have the same global importance as families comprising numerous genera from all parts of the world. Hence, the extinction of a family like the Rhynchosauridae was a major ecological event, since six species are present in the late Carnian, just before the family disappears. These species dominated their faunas and accounted for up to 70% of all tetrapod specimens found (Benton 1983) in each case. The loss of the rhynchosaurids removed a major herbivore group globally, and must have had a significant impact on the subsequent evolution of surviving herbivores, as well as predators.

The extinction of the Ornithosuchidae at the end of the Triassic, on the other hand, was a rather different matter since, by this time, it was represented by only one species (*Riojasuchus tenuiceps*), based on just four specimens from Argentina. Such a loss may have caused few ecological or evolutionary repercussions.

Some stratigraphic and taxon-counting problems could be avoided by studying a selection of local successions, i.e. sequences of faunas that span the interval of interest. The purpose of this paper is to explore the availability of Late Triassic terrestrial rock sequences that might allow studies of the postulated end-Carnian and end-Triassic mass extinction events, and to give a case study from the Germanic Basin.

## LATE TRIASSIC SEQUENCES OF THE WORLD

Numerous sedimentary sequences containing vertebrate faunas appear to span the relevant interval, in whole or in part, from the Carnian to the earliest Jurassic. These are found in Germany (the 'Keuper' succession), the south-western United States (Dockum Group, Chinle Formation), on the east coast of the United States (Newark Supergroup), in Great Britain (Lossiemouth Sandstone Formation, fissure fillings), in Argentina (Ischigualasto, Los Colorados formations), in southern Africa (Elliot, Clarens formations), and in India (Maleri, Dharmaran formations). The dating and correlation of these units is still much debated, but a tentative scheme, based on much recent work, can be given (Fig. 3).

| | | Ammonoid zones | Palynological zones | Zonations of SW German Keuper (A) | Zonations of SW German Keuper (B) | Bavaria | Thuringia |
|---|---|---|---|---|---|---|---|
| (Rhaetian) | | *Crickmayi* | Rhaetian/ Sevatian | Rhät | Rhät | Rhät | Rhät |
| **Norian** | U. | *Amoenum* | | | | | |
| | | *Cordilleranus* | | Knollenmergel | Knollenmergel | Feuerletten | Dolomitmergelkeuper/ Steinmergelkeuper |
| | M. | *Columbianus* | U.Norian (Alaunian) | Stubensandstein | U. | Burgsandstein | |
| | | *Rutherfordi* | | | | | |
| | | *Magnus* | L.Norian (Lacian) | | Stubensandstein M. | | |
| | L. | *Dawsoni* | | Kieselsandstein | | | |
| | | *Kerri* | | Rote Wand | L. | | |
| **Carnian** | U. | *Macrolobatus* | Tuvalian | Schilfsandstein | Kieselsandstein Rote Wand | Blasensandstein<br>Lehrbergschichten<br>Rote Wand | Obere Gipskeuper |
| | | *Welleri* | | Gipskeuper | Schilfsandstein | Schilfsandstein | Schilfsandstein |
| | | *Dilleri* | | | | | |
| | L. | *Nanseni* | Julian | | | | |
| | | *Obesum* | Cordevolian | | Gipskeuper | Gipskeuper | Untere Gipskeuper |
| **Ladinian** | U. | *Sutherlandi* | Langobardian | Lettenkeuper | Lettenkeuper | Grenzdolomit | Lettenkeuper |
| | | *Maclearni* | | | | | |
| | | *Meginae* | | | | | |

Fig. 3 - Stratigraphy of the Keuper (late Ladinian to Rhaetian) of the Germanic Basin. The Alpine ammonoid zones (after Tozer 1979) and palynological zones (after Visscher and Brugman 1981) are indicated as standards. Two schemes for the relative placing of the division of the Keuper in south-western Germany are noted, and scheme (B) is preferred here. The sequences in Bavaria and Thuringia are indicated in line with scheme (B). Based on data in Brenner (1973), Dockter *et al.* (1980), and Brenner and Villinger (1981).

## Germanic Basin and a global palynological standard

The German Triassic was divided into three main lithostratigraphic units, the Bunter, the Muschelkalk, and the Keuper, early in the nineteenth century, and called collectively the 'Trias' by Alberti (1834) because of this tripartite division. The Keuper succession is now considered to span from the late Ladinian (Lettenkeuper) to the end of the Triassic (Rhät).

The most complete Late Triassic successions are in Baden-Württemberg in south-west Germany, and others occur in Bavaria (Franconia), Thuringia, and in north-west Germany, as well as in NW Switzerland, Luxemburg, and Lorraine, France.

The standard stratigraphic sequence for the Triassic is based on the marine Alpine succession, where sequences of ammonoid zones have been identified (Tozer 1967, 1974, 1979).

The terrestrial sediments of the Germanic Basin are geographically close to the marine rocks of the Alps, and attempts have been made to correlate the two sequences (reviewed by Kozur 1975; Dockter *et al.* 1980), using a variety of macro - and microfossils. Kozur (1975) notes faunal and floral elements - ostracods, bivalves, gastropods, fishes, amphibians, spores, and charophytes - which are shared between Germanic basin terrestrial and brackish-water sediments, and the Alpine marine Tethys sediments.

Attempts are also being made to establish standard palynological zones for the Alpine succession that correlate with the ammonoid zones (Visscher *et al.* 1980; Visscher and Brugman 1981; Anderson 1981; Van der Eem 1983; Blendinger 1988) (see Fig. 4). Visscher *et al.* (1980) note that this scheme appears applicable to Arctic Canada, and possibly to other parts of North America as well. In particular, the Carnian phase with *Camerosporites* is detectable in North America, North Africa, and the Middle East.

While such results are encouraging, and indeed palynomorphs are well known from several horizons in the Keuper, it has not yet proved possible to establish a global standard. Problems of establishing the full stratigraphic ranges of palynomorphs exist. For example, Smith (1982) reported *Rhaetipollis germanicus* from early Norian sediments in Svalbard which had been dated independently by ammonoids to the *kerri* Ammonoid Zone of the early Norian. Previously, the widespread *Rhaetipollis* had been regarded as characteristic of the 'Rhaetian' stage.

There are other problems, both palaeogeographical and palaeoclimatological, in establishing a global palynological standard for Late Triassic stratigraphy. As Visscher *et al.* (1980, p. 285) note, the 'Angara' Flora of the Asian parts of the USSR, and the 'Gondwana' Flora from the southern hemisphere, differ from the European/ North American Floras, perhaps because of climatological differences between the regions.

Other problems relate to the description and naming of spore and pollen taxa: similar form-genera are frequently given different names if they are found in different parts of the world. Visscher *et al.* (1980), however, note a number of 'Gondwana' species that have also been found in Europe, and *vice versa,* which offers hope of the possibility of global correlations of terrestrial sediments. When the Alpine/ Germanic palynological record is fully documented and correlated with the ammonoid zones, it is likely that global correlations of terrestrial Triassic sediments will be much improved.

There are currently two ways of interpreting the position of the Carnian/ Norian boundary in the German Keuper (Fig. 3). According to interpretation (A), the Rote Wand and Kieselsandstein are early Norian in age (Geiger and Hopping 1968; Fisher 1972; Fisher and Bujak 1975; Dunay and Fisher 1979; Dockter *et al.* 1980; Anderson 1981; Schröder 1982), while according to interpretation (B), those two horizons are late Carnian (Kozur 1975; Gall *et al.* 1977; Olsen *et al.* 1982). Palaeoclimatic evidence tends to favour interpretation (B), according to Dockter *et al.* (1980, p. 960). The Obere Gipskeuper (= Rote Wand + Kieselsandstein, or Rote Wand + Blasensandstein) contains numerous evaporitic horizons, some of which carry gypsum, which is true also of the southern Alpine Torrer Schichten, Opponitzer Rauhwacke, and Raibler Gips of Austria. The Opponitzer beds are dated as uppermost Carnian (Tuvalian) by their brackish-water fauna, via ammonoids and palynomorphs, and the Oberer Gipskeuper is given the same date by its rich ostracod fauna, including *Costatoria vestita* (Dockter *et al.* 1980). The remaining gypsiferous horizons of the Alpine and Germanic basins are then correlated on palaeoclimatic grounds. Magnetostratigraphic evidence, on the other hand, indicates that the Schilfsandstein is latest Carnian in age (Hahn 1982), and this favours interpretation (A). In this paper, interpretation (B) is followed; if (A) had been selected, the results would have been little changed. Other aspects of the dating in detail of the Keuper are still unclear: for example, the lower boundary of the Gipskeuper, in north Württemberg at least, falls in the uppermost Ladinian (Bachmann and Gwinner 1971).

Fossil vertebrates have been reported from numerous horizons throughout the Keuper successions of Germany, especially from the Baden-Württemberg region, where faunas have been noted from 12 or more horizons spanning from the Lettenkeuper (late Ladinian) to the Rhät ('Rhaetian'). There are, however, few finds from the Carnian parts of the sequence.

The Keuper rock succession is largely terrestrial, consisting of great thicknesses of sandstones and mudstones with intervening marine limestones, dolomites, and evaporite deposits (Gipskeuper). The successions are up to 1750 m thick in the classic Germanic basins (Schröder 1982). The only major unconformity is the 'Altkimmerische Discordanz', accounting for about 600 m of erosion at most (Bouman 1982), and lying between the Obere Gipskeuper and the Dolomitmergelkeuper, in other words at the lower/middle Norian boundary according to interpretation (A) or at the Carnian/ Norian boundary according to interpretation (B) (see Figure 3).

The German basin sequence is interrupted by many smaller unconformities, and depositional rates varied greatly. Although no major span of Late Triassic time is missing, the Germanic sequence is not adequate for a precise test of the effects of a late Carnian or an end-Triassic extinction event since, for the former, there are so few Carnian tetrapods known from the sequence, and for the latter, there is a major facies change during, or at the end of, the Rhätkeuper (terminal Triassic), when a major marine regression occurred, terminating terrestrial sedimentation in the Germanic basin.

## South-western United States

The Late Triassic of Arizona, New Mexico, Texas, Utah, Colorado, and Wyoming is extensive in outcrop and includes a number of major basins of terrestrial sedimentation. Most of the relevant tetrapod-bearing horizons belong to the Chinle Formation or the Dockum Group, but there are many local stratigraphic names for members and formations, and correlations are complex. There is also a wide range of opinions on the stratigraphic range and dating of the Chinle and the Dockum: Olsen and Sues (1986) regard most, if not all, of both units as being late Carnian or late Carnian to early Norian in age, while Parrish (1989), Dubiel *et al.* (1991), Hunt and Lucas (1991a, b), and others, regard both as spanning a much longer interval of time, from the late Carnian to the late Norian.

Dunay and Fisher (1979) assigned a late Carnian age to all Dockum palynological samples which they studied, while Gottesfeld (1980) reported a similar conclusion for both the Dockum and the Chinle. Litwin (1985) suggested a late Carnian (Tuvalian) age for palynomorphs sampled from the Petrified Forest and Monitor Butte members of the Chinle Formation. On the other hand, Ash (1989) gives a late Carnian to early Norian age for both the Chinle Formation and the Dockum Group, based upon megaplants and palynomorphs.

The most comprehensive study to date, by Litwin *et al.* (1991), gives a broad range of ages for the Chinle Formation, from late Carnian to early Norian, and possibly late Norian (Fig. 4). These authors subdivide the Chinle palynomorphs into three successive zones, Zones I and II falling in the Tuvalian (late Carnian), and Zone III falling in the early (?-late) Norian. Samples from the Temple Mountain Member of southern Utah gave a Zone I age. Samples from the Shinarump, Monitor Butte, and Moss Back members, the lower part of the Petrified Forest Member, and the Sonsela Sandstone of southern Utah, north-eastern Arizona, and northwestern New Mexico were all assigned to Zone II, equivalent to the later Tuvalian. The lower portions of the Dockum Group of Texas and New Mexico, sampled by Dunay and Fisher (1979) probably also belong here. Samples from the upper part of the Petrified Forest Member of north-eastern Arizona and southern Utah are assigned to the lower part of Zone III, corresponding to the earliest Norian. Samples from lateral correlatives in southern Utah of the Church Rock and Owl Rock members of the Chinle indicate a post-late Carnián, but pre-latest Norian age. Dunay and Fisher (1979) refer to the named formations as early Norian, although they cannot exclude a middle or late Norian (pre 'Rhaetian') age. There is then an unconformity before the onset of the Hettangian (earliest Jurassic) Moenave Formation. More sampling from the upper parts of the Chinle sequence would be helpful in resolving this upper age-limit problem, but Litwin *et al.* (1991) have found that samples taken to date from the Owl Rock and Church Rock members are palynologically barren.

Work by Ash (1980, 1989) on megaplant fossils also suggests a range of Carnian and Norian ages for the Chinle Formation. He established a sequence of floral assemblages in the North American Late Triassic and Early Jurassic, namely: (1) Zone of *Eoginkgoites* (middle Carnian), (2) Zone of *Dinophyton* (late Carnian), (3) Zone of *Sanmiguelia* (Norian-'Rhaetian'), and (4) an unnamed zone (Rhaeto-Liassic). *Sanmiguelia,* for example, is recorded from the Tru-

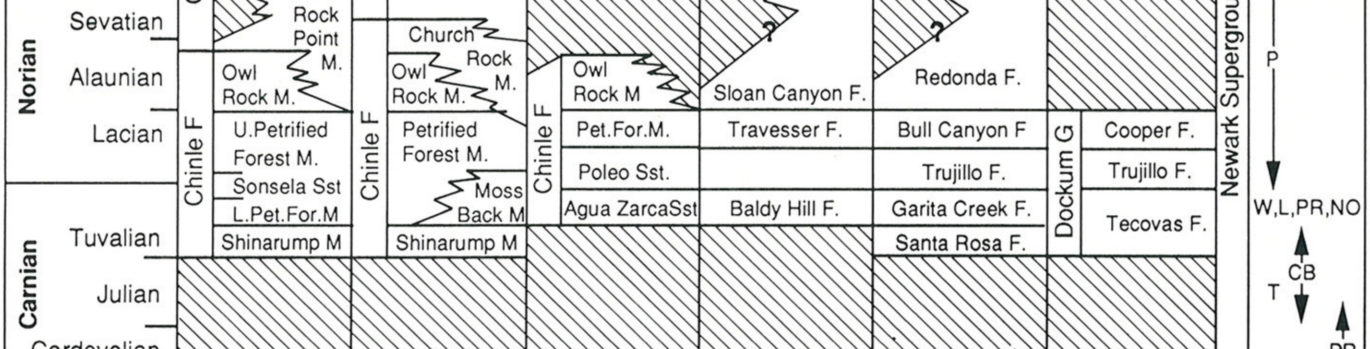


Fig. 4 - Stratigraphy of some vertebrate-bearing sequences in North America. The expansion of the Chinle Formation and the Dockum Group through the late Carnian and much of the Norian is based on comparisons of tetrapods with the German sequence by Olsen and Sues (1986), Hunt and Lucas (1990, 1991a, b), and others, and on palynological work by Litwin *et al.* (1991). Abbreviations: CB, Cow Branch Formation; L, Lockatong Formation; M, McCoy Brook Formation; NH, New Haven Arkose; NO, New Oxford Formation; P, Passaic Formation; PK, Pekin Formation; PT, Portland Formation; T, Turkey Branch Formation; W, Wolfville Formation.

jillo Formation of Texas, the Owl Rock Member (Chinle Formation) of Utah, and the Rock Point Member (Glen Canyon Group) of Arizona, hence confirming a Norian age (Ash 1989).

Evidence from vertebrates (papers in Lucas and Hunt 1989; Hunt and Lucas 1990, 1991a, b), especially the phytosaurs and stagonolepidids, confirms Litwin *et al.*'s (1991) findings, and points to the strong likelihood of middle, and even late, Norian ages for the upper parts of the Chinle Formation. Many of the reptiles are closely comparable with finds from the middle Stubensandstein of Germany (middle Norian), and others point to the possible presence of later stages (Hunt and Lucas 1990).

The Chinle Formation and Dockum Group are 300-550 m thick, not a great thickness if, for example, the Chinle spans the late Carnian and much of the Norian. There is no evidence for long-term unconformities, and vertebrates are found throughout all sequences shown in Figure 4. Hence, if biostratigraphic relationships can be established independently of vertebrate fossils, the Chinle Formation and Dockum Group could be important units in which to test the effects of a postulated late Carnian extinction event. In addition, the sequences appear to continue across the Triassic/Jurassic boundary in north-eastern Arizona and southern Utah, after the transition from the Chinle Formation to the Glen Canyon Group, so a test of the effects of a postulated end-Triassic event may also be possible. So far, the stratigraphy has not been worked out sufficiently, and faunal compositions through time have not been reviewed in enough detail for such tests, but Hunt (1991) has made a first attempt.

### Eastern North America

The Newark Supergroup, distributed in more than 20 basins along the Atlantic coast of the United States and Canada, from South Carolina to Nova Scotia, documents most of the Late Triassic and Early Jurassic. The most complete single succession, in the Newark Basin of Pennsylvania, New Jersey, and New York, covers a time span from the middle Carnian to the Pliensbachian in 6000 m of lacustrine sediments (Olsen 1980; Olsen *et al.* 1982, 1989). It has been argued that this is the world's best sequence for documenting vertebrate turnovers during this time interval (Olsen and Sues 1986; Olsen *et al.* 1987, 1988, 1991; Hallam 1990).

Known tetrapod skeletal faunas from the Newark Supergroup at present offer little hope of detailed documentation of the postulated late Carnian and end-Triassic extinction events. Certainly, the presence of an earliest Jurassic fauna from the McCoy Brook Formation of Nova Scotia gives an useful guide to the results of a postulated end-Triassic event (Olsen *et al.* 1987, 1988; Shubin *et al.* 1991), but immediately preceding latest Triassic faunas are poorly known in the region.

The known tetrapod skeletal faunas are as follows (Fig. 4): early to middle Carnian (the Pekin Formation of the Deep River Basin, North Carolina; the Turkey Branch Formation of the Richmond Basin, Virginia; and the Stockton Formation of the Newark Basin, Pennsylvania and New Jersey), middle to late Carnian (the Cow Branch Formation of the Dan River Basin, North Carolina; the Lockatong Formation of the Newark Basin, Pennsylvania and New Jersey; and the middle and upper Wolfville Formation of the Fundy Basin, Nova Scotia), Norian (the Passaic Formation of the Newark Basin, Pennsylvania and New Jersey; and the New Haven Arkose of the Hartford Basin, Connecticut). Skeletal fossils from the Carnian units are relatively abundant, but the Passaic Formation and the New Haven Arkose have yielded only sparse remains, amounting to about ten specimens of aetosaurs, phytosaurs, procolophonids, prosauropods and others in total (Olsen 1980). Such are hardly sufficient to characterise Norian tetrapod evolution, nor to delimit the after-effects of a postulated late Carnian extinction, nor the lead-up to an end-Triassic event.

Tetrapod footprint assemblages throughout the whole Carnian to Early Jurassic interval of the Newark Supergroup are much richer, and offer the potential for detailed documentation of faunal changes when they can be correlated to a more precise standard stratigraphic scale. The main problem will be in matching footprints to alleged trackmakers, a difficult task (Olsen and Baird 1986; Olsen *et al.* 1991). Indeed, it is probably unwise to extend familial durations on the basis of footprint evidence alone. Silvestri and Olsen (1989), for example, report *Rhynchosauroides* from the Norian of Pennsylvania, although apparently after the global extinction of rhynchosaurs in the late Carnian, as indicated by skeletal fossils. It is in the nature of all trace fossil taxa that nearly identical tracks can be produced by entirely unrelated animals. Tracks assigned to *Rhynchosauroides* have likely been made by a wide range of terrestrial lepidosauromorphs.

### Great Britain

The Lossiemouth Sandstone Formation of Elgin, Scotland, is dated as late Carnian on the basis of its extensive reptilian fauna which includes such key taxa as the rhynchosaur *Hyperodapedon* and the aetosaur *Stagonolepis* (Benton and Walker 1985; Hunt and Lucas 1991b). It has yielded no other kinds of fossils and can be dated only as post-Early Triassic and pre-Rhaetian on regional lithostratigraphic grounds.

A potentially more useful sequence of faunas for determining the nature of any Triassic-Jurassic event are those from the fissure and cave fills of South Wales and the Bristol region. One of these has been dated palynologically as Rhaetian (Marshall and Whiteside 1980), and others as Sinemurian (formerly 'Rhaeto-Liassic') (Evans 1980; Kermack *et al.* 1973). The fissures have been said to contain two kinds of vertebrate faunas, a Late Triassic one dominated by reptiles, and a Rhaeto-Liassic one with specimens of mammals and tritylodonts. The older fissures have yet to yield non- vertebrate evidence of age, but Simms (1990) regards them all as post-middle Carnian by dating the formation of the caves. In addition, certain faunal elements imply a date as old as late Carnian for some fissure fills. For example, the flying diapsid *Kuehneosaurus,* found in several fissures, is very like *Icarosaurus* from the late Carnian Lockatong Formation of New Jersey. In addition, the procolophonid *Leptopleuron* from one fissure is nearly identical with representatives of that genus from the Lossiemouth Sandstone Formation (N. C. Fraser, pers. comm., 1991). Other fissures have produced the crocodilomorph *Terrestrisuchus,* very like *Saltoposuchus* from the Middle Norian Stubensandstein of Germany (Fraser 1986), and in fact considered synonymous by Clark in Benton and Clark (1988). It may be that the fissures will provide a series of excellent late Carnian to Sinemurian faunas for studies of postulated extinction events, but their total stratigraphic distribution will probably remain patchy.

### Argentina

The Ischigualasto Basin, in the Provinces of La Rioja and San Juan in northwestern Argentina, contains a sequence of sediments dated as middle to latest Triassic (Bonaparte 1978, pp. 213-221, 1982), which are apparently largely conformable and continuous. The contained tetrapods indicate Ladinian, latest Carnian, and early to late Norian ages for the Ischichuca, Ischigualasto, and Los Colorados formations respectively (Fig. 5).

Radiometric ages from volcanics overlying the Ladinian and Carnian reptile assemblages in the Ischigualasto-Ischichuca Basin give a K-Ar mean age of 229±5 Ma (Gonzalez and Toselli 1975), hence early Carnian according to Forster and Warrington (1985). Palynological work on the Argentinian sequence is limited, and has not provided strong evidence for age interpretation (e.g. Herbst 1970), although megafossil plants and spores suggest a Carnian age for the Ischigualasto Formation.

Bonaparte (1978, 1982) indicates that the succession from the Ischichuca Formation to the Los Colorados Formation is relatively continuous, and especially notes the continuity between the Ischigualasto and Los Colorados Formations, where a specimen of the dicynodont *Jachaleria* was found at the junction of the two. The La Esquina local fauna of the Los Colorados Formation of dinosaurs, crocodilomorphs, and mammal-like reptiles is generally dated as latest Triassic by faunal comparison, although Olsen and Sues (1986, p. 326) hint that the fauna may be a mixture of latest Triassic and earliest Jurassic elements. However, Bonaparte (1978, p. 220) notes that all the La Esquina tetrapods came from the top 100 m of the 800 m - thick Los Colorados Formation, which suggests that it is truly a single fauna.

The whole Late Triassic succession in Argentina is about 1500 m thick, and if tetrapod fossils were found more commonly in the lower parts of the Los Colorados Formation, this could be used to study the postulated late Carnian event. At present, there is no evidence for a continuation of the sequence into the Early Jurassic, and so studies cannot be made of the impact of the postulated end-Triassic event.

### India

A sequence of Late Triassic and Early Jurassic vertebrate-bearing sediments is well known from the northern Pranhita-Godavari Valley of north-central India (Kutty *et al.* 1987; Kutty and Sengupta 1989). The Bhimaram Sandstone (?Ladinian), which has produced only sparse tetrapod remains, is overlain by the Maleri Formation. The Maleri has yielded extensive faunas which have generally been dated as late Carnian. However, Kutty and Sengupta (1989) have identified two distinct Maleri faunas, a lower and an upper one, which are clearly not the same age. The lower Maleri fauna consists of fishes, metoposaurs, *Malerisaurus, Hyperodapedon, Paleorhinus,* an aetosaur, a large dicynodont, *Exaeretodon,* and a possible prosauropod. These, particularly the phytosaur *Paleorhinus* and the rhynchosaur *Hyperodapedon* , apparently confirm an early late Carnian age (Hunt and Lucas 1991a). The upper Maleri fauna, with fishes, temnospondyls, the phytosaur *Rutiodon,* an aetosaur, a phytosaur, and a large dicynodont, is probably latest Carnian, belonging to the *Rutiodon* biochron of Hunt and Lucas (1991a), although Kutty and Sengupta (1989) suggest an early Norian age.

The Maleri Formation is overlain by the Dharmaram Formation, which was once regarded as a single

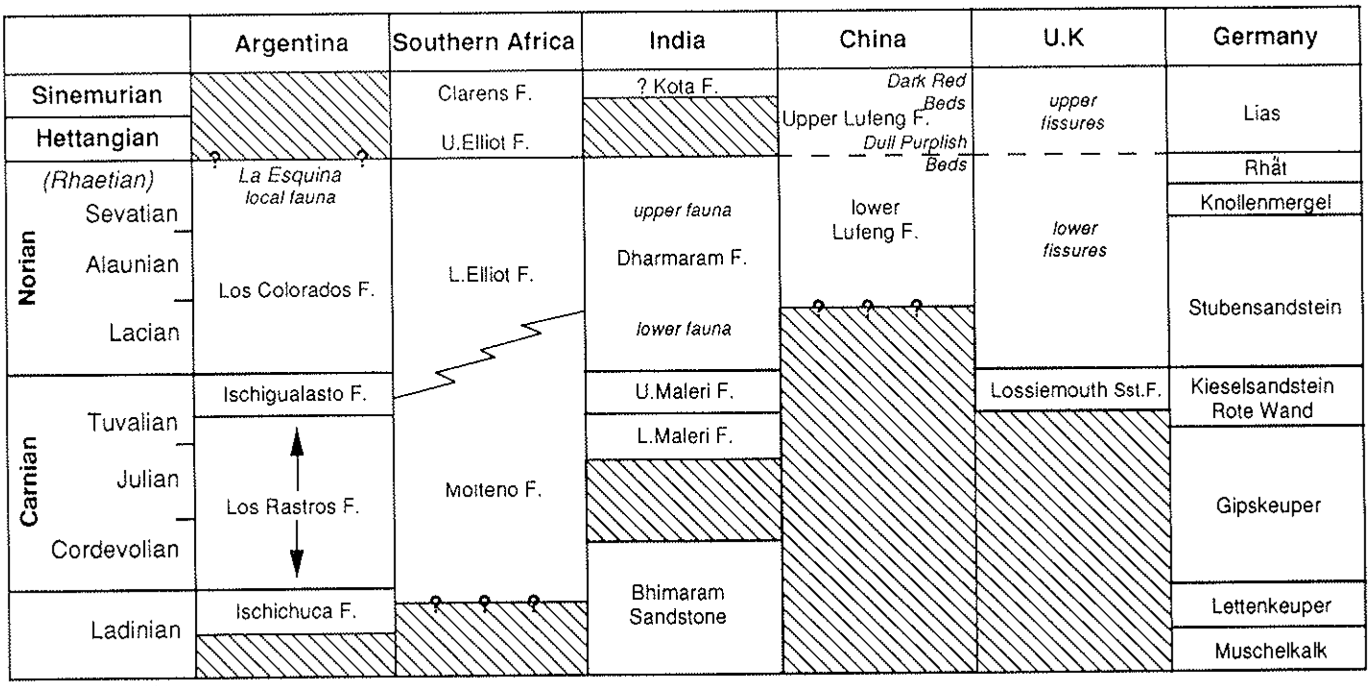


Fig. 5 - Stratigraphy of vertebrate-bearing sequences in the Late Triassic and earliest Jurassic of various parts of Gondwanaland. The dates are based largely on comparisons of tetrapods with the German sequence by Olsen and Sues (1986) and others, with some sporadic information from palynology, invertebrates, and absolute age dates.

unit, but which has also yielded two distinctive faunas, according to Kutty and Sengupta (1989). The lower fauna, consisting of fishes, *Nicrosaurus*, ? *Paratypothorax,* and small prosauropods, seems to be early Norian in age, and equivalent to the Trujillo Formation of the Dockum Group of Texas and New Mexico, and the Sonsela Sandstone Bed and Poleo Member of the Chinle Formation of New Mexico and Arizona (Hunt and Lucas 1990). The upper Dharmaram fauna consists of an ? ornithosuchid, a sphenosuchid, a small prosauropod, and a plateosaurid, indicating a late Norian age, possibly equivalent to the German Knollenmergel. This is succeeded by the Kota Formation with dinosaurs and other vertebrates that suggest an Early Jurassic age (? post-Hettangian).

The rhynchosaur *Hyperodapedon huxleyi* occurs in both the Maleri Formation and the Tiki Formation of Madhya Pradesh. The latter has been dated as Carnian to Norian through palynological studies (Kumaran and Maheshwari 1980), but much more precise palynological work on this, and the other tetrapod-bearing formations of India is required.

The Pranhita-Godavari sequence of the Maleri, Dharmaram, and Kota formations is 1230 m thick (Yadagiri and Rao 1987), and appears to be relatively uninterrupted, except for a significant unconformity between the top of the Dharmaram and the base of the Kota. The sediments of all three formations (Kutty *et al.* 1987; Yadagiri and Rao 1987) appear to represent a mixed fluviatile / lacustrine regime with occasional calcrete development in alternating monsoonal and arid conditions. The sequences might be adequate to test the effects of a postulated late Carnian event, since the lower part of the Dharmaram Formation seems to be early Norian in age, but the earliest Jurassic hiatus precludes any detailed studies of the aftermath of a postulated end-Triassic event.

### Southern Africa

The old 'Red Beds' and 'Cave Sandstone', jointly the 'Stormberg Beds', and now the Elliot and Clarens formations respectively, were long regarded as Late Triassic in age, but have been significantly redated to lie largely in the Early Jurassic (Olsen and Galton 1977, 1984). They contain several faunas of dinosaurs, mammal-like reptiles, and footprints (Olsen and Galton 1984). The underlying Molteno Formation has yielded megaplant fossils, insects, conchostracans, and fishes, but no tetrapod remains. The megaflora and palynoflora indicate a late Carnian age for at least part of the Molteno (Anderson and Anderson 1984). Kitching and Raath (1984) divided both the Elliot and Clarens Formations into lower, middle, and upper units respectively. The lower Elliot Formation is characterised by an abundance of the prosauropod *Euskelosaurus,* as well as the mammal-like reptile *Scalenodontoides,* capitosaurid temnospondyls, and (?) rauisuchids, which all point to a Norian age. The remainder of the Elliot Formation, and the whole of the Clarens, is characterised by Early Jurassic (Hettangian-Sinemurian) reptile remains. Olsen and Galton (1984) accept these ages for the Elliot and Clarens Formations based upon tetrapod footprints as well as skeletal remains. The sequence is capped by the Drakensberg volcanics which have yielded radiometric ages of 114-194 Ma (Visser 1984), the oldest age being confirmed as 193±3 Ma for the onset of Karroo volcanism by Forster and Warrington (1985). This places the Clarens/Drakensberg contact close to the Sinemurian/Pliensbachian boundary.

Clearly, more palynological studies are needed in order to divide the Stormberg Beds and confirm their age distribution. The Elliot and Clarens Formations together are only 250 m thick (Kitching and Raath 1984), but could provide evidence on both post-Carnian and Triassic/Jurassic boundary events.

### China

The Lower Lufeng Formation of Yunnan, China also appears to straddle the Triassic/ Jurassic boundary, having formerly been entirely assigned to the Late Triassic. The Dark Red Beds and underlying Dull Purplish Beds of the Lower Lufeng Formation have yielded diverse crocodilomorphs, prosauropods, ornithischians, mammal-like reptiles, and mammals, all of typical Early Jurassic type (Sun and Cui 1986). The age is confirmed by finds of indicator ostracods and molluscs. The Dull Purplish Beds may or may not extend down into the uppermost Triassic (Zhen *et al.* 1985), but the lower extent of these is uncertain. Clearly, this 750 m-thick sequence of highly fossiliferous sediments could be very useful in testing mass extinction hypotheses if it actually spans the Triassic / Jurassic boundary.

## TETRAPOD FAUNAL CHANGE IN THE LATE TRIASSIC OF SW GERMANY

### The tetrapods

Fossil tetrapods have been known from the Keuper of south-west Germany for some time. G. Jaeger described both *Mastodonsaurus* and *Phytosaurus* from the River Neckar and Hohenlohe area in 1828. Hermann von Meyer published numerous works on Keuper reptiles, and named *Plateosaurus* (1837), *Belodon* (1842), *Tanystropheus* (1847-55), and *Teratosaurus* (1861). Th. Plieninger also published extensively on the Württemberg Triassic at this time, and named *Zanclodon* (1846) and several Rhät ('Rhaetian') reptiles. Towards the end of the 19th century, Oscar Fraas, and his son Eberhard, continued the work. O. Fraas named *Nicrosaurus* (1866), *Dyoplax* (1867) and *Aetosaurus* (1877), and E. Fraas named *Cyclotosaurus* (1889), *Mystriosuchus* (1896), and *Proterochersis* (1913).

In the 20th century, Friedrich von Huene was particularly active in describing and excavating in the Baden-Württemberg Triassic. Much of the history of this subject is reviewed by Kuhn (1971), Brenner (1973), and Wild (1991).

Several authors have reviewed elements of the German Keuper fauna recently, for example the temnospondyl amphibians (Milner 1993), the turtles (Gaffney 1990), the phytosaurs (Westphal 1976), the aetosaurs (Walker 1961), the rauisuchians (Galton 1985a; Benton 1986c), the dinosaurs (Galton 1985a, b), the cynodonts (Hahn *et al.* 1987), and the mammals (Clemens 1980). However, there has been no systematic survey of the entirety of the faunas.

## Geology

The stratigraphy of the Germanic Keuper has been outlined above. Fossil tetrapods have been collected at more than 75 localities in the Keuper of Baden-Württemberg in a strip that runs from Heilbronn and Schwäbisch Hall in the northeast to Donaueschingen in the southwest (Fig. 6). The most abundant finds come from the general areas of Stuttgart and Tübingen, and recent discoveries have generally been made on construction sites and road-building works. The Keuper deposits continue NE into Franconia and Thuringia, and SW into Switzerland and E into Lorraine and Luxembourg, where further similar reptile finds have been made. However, most tetrapod remains have come from the Baden-Württemberg Keuper, and the present study is restricted to that area.

The lithostratigraphy of the Keuper in Baden-Württemberg has been the subject of a great deal of study, and over 550 sections have been taken in quarries and boreholes. This large amount of information has enabled geologists to correlate distinctive lithological horizons throughout the basin (e.g. Brenner 1973, 1978a, b), to draw up standard lithostratigraphic sections (e.g. Brenner and Villinger 1981; Gwinner 1980), and to reconstruct regional palaeogeography at different times during the filling of the basin (e.g. Brenner 1973, 1979). A typical section (Fig. 7) shows the following lithologies: mudstones with dolomitic marl beds and occasional channel sands in the Lettenkeuper, mudstones with thin limestone and gypsum-bearing beds in the Gipskeuper, thick sandstones in the Schilfsandstein, red, green, and dark marls and mudstones in the Rote Wand/Obere Bunte Mergel, with thick sandstones between (Kieselsandstein), massive red sandstones interbedded with mudstones and siltstones and occasional calcretes in the Stubensandstein, thick red marls with occasional limestones in the Knollenmergel, and light-coloured sandstones and mudstones in the Rhät.

Throughout Keuper times, the Baden-Württemberg area was a deltaic plain (Fig. 8). The Muschelkalk sea had withdrawn to the west and north - the Lettenkeuper is a transitional marine and brackish-water deposit and the Gipskeuper is mainly marine - the rest of the Keuper was deposited in fresh water. Rivers flowed north and west over the plain from ancient mountain ranges in southern Bavaria, Bohemia and Austria, and these deposited vast channel sands. The coloured mudstones of the Rote Wand and Bunte Mergel were deposited in an arid desert-like environment which seldom yield animal or plant fossils. The remainder of the Keuper also shows signs of arid conditions - gypsum deposits, salt pseudomorphs, and calcretes. The landscape may have been dotted with oasis-like pools which were surrounded by ginkgos, cycads, and conifers, and temporary pools and rivers that were populated by ostracods, mussels, freshwater fishes like *Semionotus* and the lungfish *Ceratodus*. On the banks of these water bodies lived phytosaurs, temnospondyl amphibians, and turtles, while the medium- to large-sized dinosaurs appeared later and wandered more widely. Tetrapod remains have been found at many levels in the Keuper, and these are indicated in Figure 7.

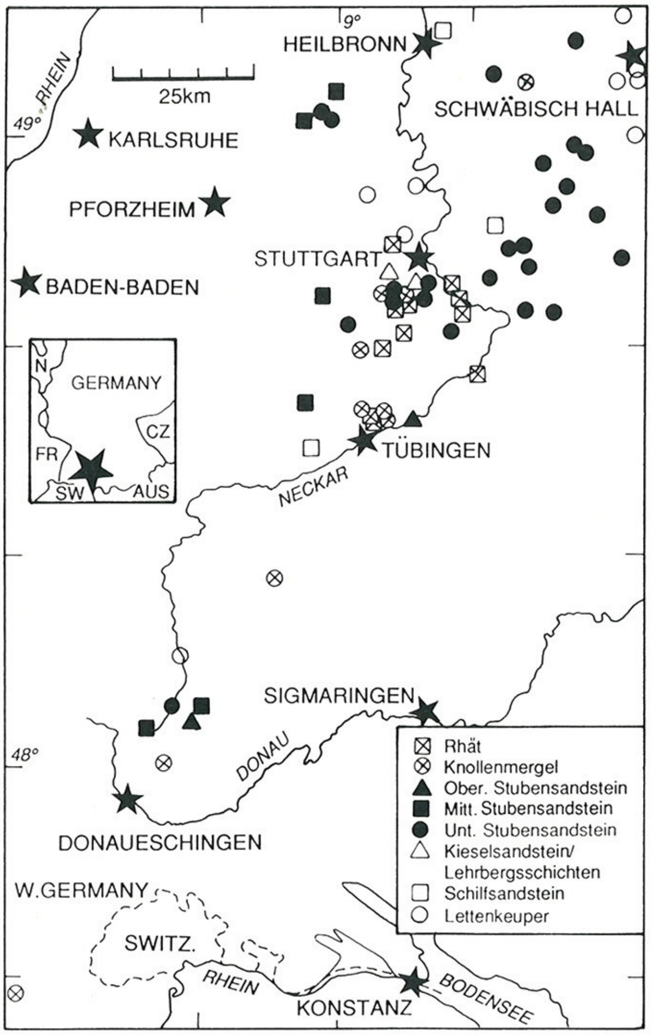


Fig. 6 - Localities in south-western Germany that have yielded tetrapod faunas from the Keuper. The main rivers and towns are indicated, and locality symbols are coded according to stratigraphyc age (see diagrammatic key). The data come from the palaeontological collections in Stuttgart and Tübingen, and from the literature. A base map of central Europe indicates the area shown. Abbreviations: AUS, Austria; CZ, Czechoslovakia; FR, France; N, Netherlands; SW, Switzerland. Based on a map in Benton (1986a).

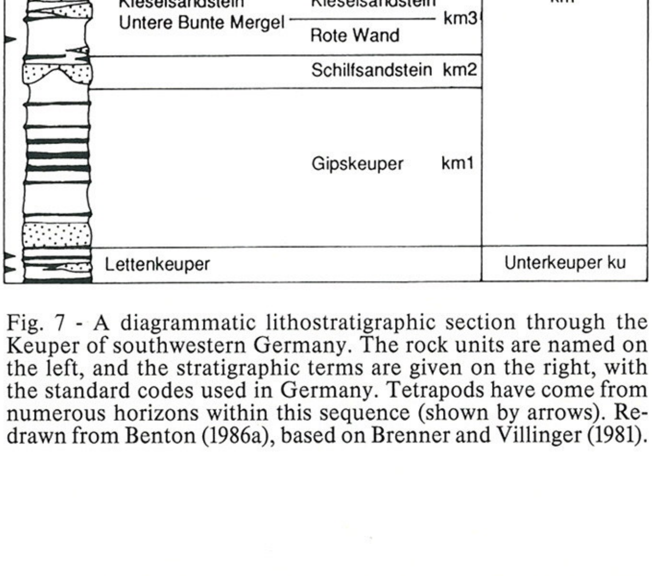
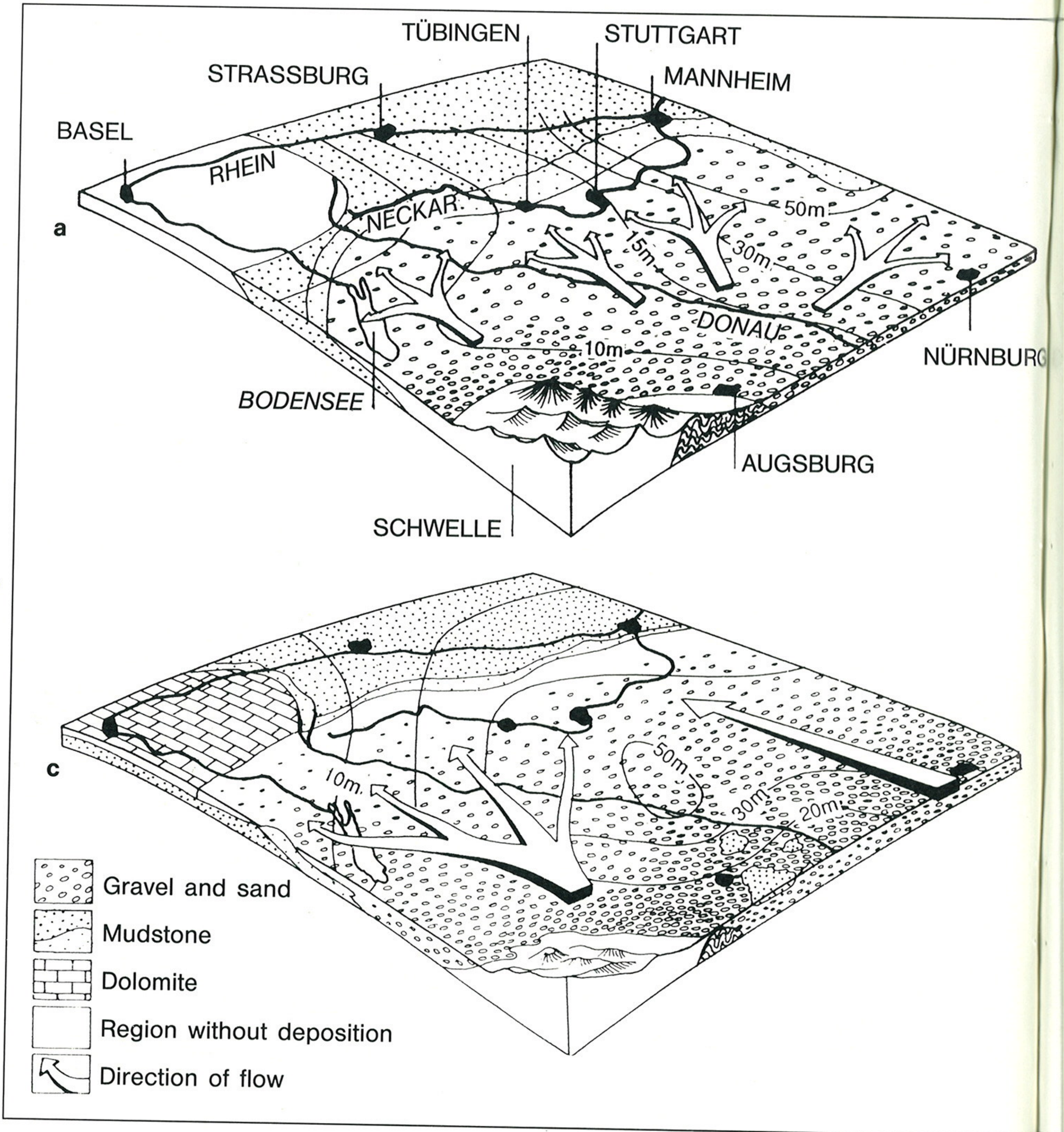


Fig. 7 - A diagrammatic lithostratigraphic section through the Keuper of southwestern Germany. The rock units are named on the left, and the stratigraphic terms are given on the right, with the standard codes used in Germany. Tetrapods have come from numerous horizons within this sequence (shown by arrows). Redrawn from Benton (1986a), based on Brenner and Villinger (1981).



## Tetrapod faunal successions through the Keuper

Data were collected on the precise localities and stratigraphic horizons of the majority of Keuper amphibians and reptiles from Baden-Württemberg. This was done by visits in March and April 1982 to the major collections in Stuttgart and in Tübingen, as well as to smaller collections in München, Erlangen, Göttingen, Berlin, and London. Locality and stratigraphic data were recorded from labels and other documents associated with specimens. Localities were then identified more precisely by reference to high-scale geological and topographic maps in the libraries attached to the museums in Stuttgart and Tübingen. Geological memoirs gave precise locality information in some cases, but only in those issued recently. I also visited a number of localities. The Appendix shows all the localities arranged stratigraphically, and gives details of the fauna, the approximate numbers of individual animals of each taxon represented, any documentary or published information on the locality, and, where possible, a map reference.

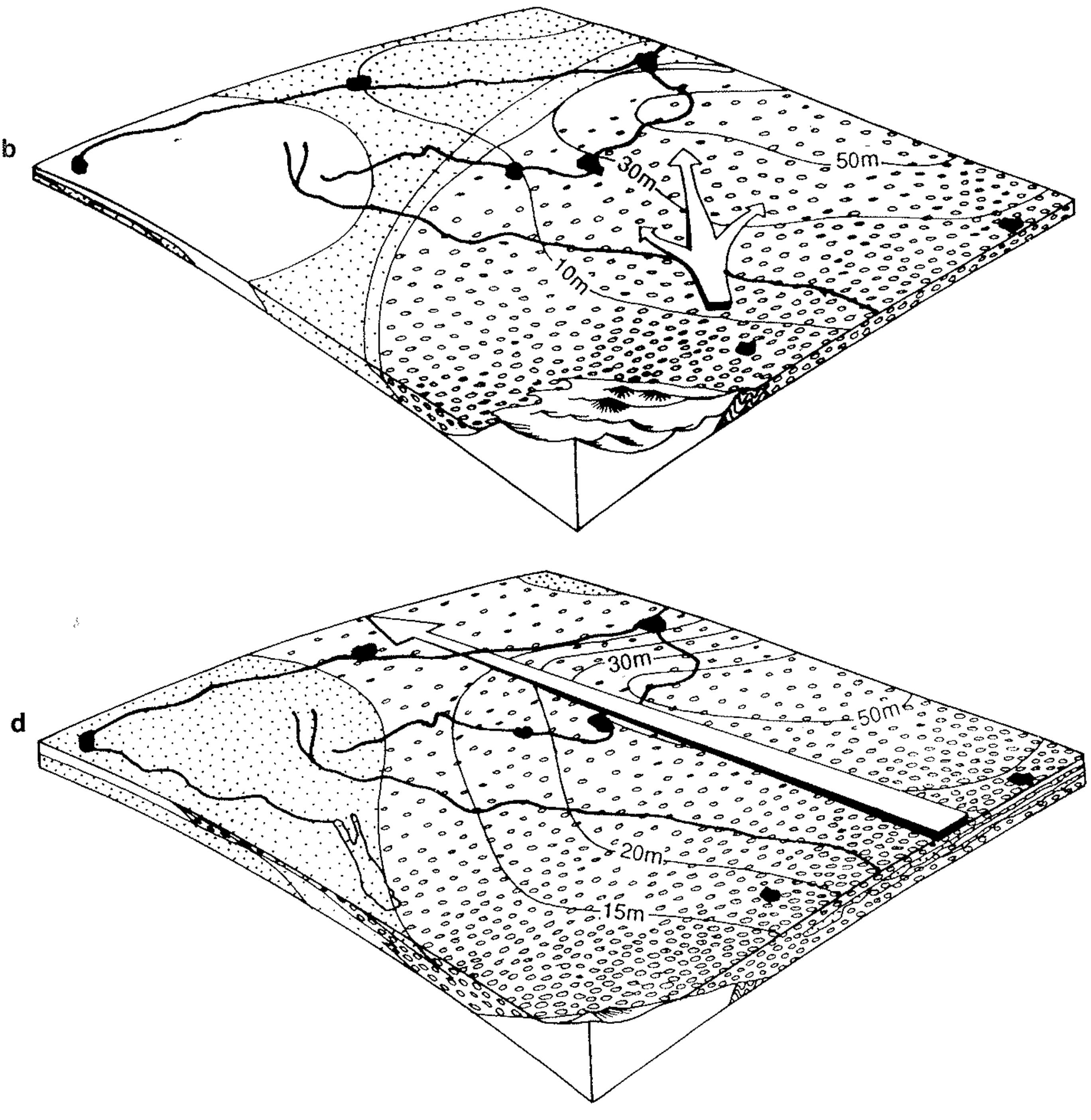


Fig. 8 - Palaeogeographic views of south-western Germany during four phases of the Late Triassic, the times of deposition of (a) the Kieselsandstein, (b) the Unterer Stubensandstein, (c) the Mittlerer Stubensandstein, and (d) the Oberer Stubensandstein. There was no substantial change in depositional regime during this late Carnian to late Norian interval. Based on Brenner (1979).

Summaries of the 'typical' faunas of each stratigraphic unit were attempted, based on combinations of specific localities. The numbers of individual examples of each taxon were totalled for the stratigraphic unit (Table 1), and converted to percentages of the fauna, where the numbers permitted. Few vertebrates have been found in the Gipskeuper or the Rote Wand, and totals from the Kieselsandstein and the Lehrbergschichten are too small to allow valid calculation of percentages. In addition, percentage estimates were not made for the faunas of the Rhät bonebeds, because the nature of their preservation is so different from that of the rest of the Keuper.

The results have been presented before, in summary form (Benton 1984, 1986a; reviewed Hunt 1991), and are given in Figure 9. The changes in values during the Ladinian and Carnian are probably not significant in evolutionary terms, since the preservation of faunas is so patchy. However, the Stubensandstein and Knollenmergel record, spanning most of the Norian, is much more useful since it is based on a large range of rich localities, and it re-

Table 1 - Non-marine tetrapod faunas from the Keuper (latest Middle to Triassic) of Baden-Württemberg, south-western Germany. The data are based mainly on the collections in Stuttgart and Tübingen, with percentages of faunas for the Lettenkeuper from Wild (1980). Modified from the tabulation in Benton 81986a, p. 309) as a result of new information from R. Wild (pers. comm., 1992).

| | | **No.** | **% of fauna** |
|---|---|---|---|
| **Lettenkeuper** | | | |
| TEMN | *Gerrothorax* | ? | 12 |
| | *Mastodonsaurus, etc.* | ? | 65 |
| PROL | *Tanystropheus, etc.* | ? | 2 |
| THEC | rauisuchid indet. | ? | 9 |
| THER | small ?cynodonts | ? | 12 |
| **Schilfsandstein** | | | |
| TEMN | *Metoposaurus* | 30+ | 49 |
| | *Cyclotosaurus* | 30+ | 49 |
| THEC | *Belodon* | 1 | |
| | *Dyoplax* | 1 | 2 |
| | indet. | 1 | |
| **Lehrbergschichten** | | | |
| TEMN | *Metoposaurus* | 4 | 50 |
| | *Plagiosaurus* | 1 | 12 |
| | ?*Cyclotosaurus* | 1 | 12 |
| THEC | *Belodon* | 2 | 26 |
| **Kieselsandstein** | | | |
| THEC | *Phytosaurus* | 1 | 50 |
| | rauisuchian | 1 | 50 |
| **Unterer Stubensandstein** | | | |
| TEMN | *Cyclotosaurus* | 2 | 2 |
| | *Plagiosaurus* | 1 | 1 |
| TEST | *Proterochersis/Proganochelys* | 20 | 20 |
| THEC | *Teratosaurus/Postosuchus* | 6 | 6 |
| | *Nicrosaurus, etc.* | 42 | 41 |
| | *Aetosaurus/Paratypothorax* | 25 | 25 |
| PROS | *Sellosaurus* | 4 | 4 |
| | *Thecodontosaurus* | 1 | 1 |
| **Mittlerer Stubensandstein** | | | |
| TEMN | *Cyclotosaurus* | 29 | 23 |
| | *Gerrothorax* | 3 | 2 |
| TEST | *Proganochelys* | 3 | 2 |
| THEC | *Aetosaurus* | 4 | 3 |
| | *Teratosaurus* | 12 | 9 |
| | phytosaurs | 38 | 30 |
| CROC | *Saltoposuchus* | 5 | 4 |
| PROS | *Plateosaurus/Sellosaurus/'Efraasia'* | 22 | 17 |
| | *Thecodontosaurus* | 4 | 3 |
| CERA | *Procompsognathus* | 2 | 2 |
| | *Halticosaurus* | 5 | 4 |
| | theropod | 1 | 1 |
| **Oberer Stubensandstein** | | | |
| TEST | *Proganochelys* | 3 | 4 |
| THEC | *'Phytosaurus'* | 1 | 1 |
| PROS | *Plateosaurus* | 62 | 95 |
| **Knollenmergel** | | | |
| PROS | *Plateosaurus/Sellosaurus* | 27 | 100 |

cords the faunas of an environmentally more uniform time period.

The proportion of dinosaurs present rises from 5% in the Lower Stubensandstein, to 27% in the middle, 95% in the upper, and 100% during Knollenmergel times. During the same time, turtles declined in abundance from 20% in the lower Stubensandstein to 2% in the middle, 4% in the upper, and 0% in the Knollenmergel. Temnospondyl amphibians increased in relative abundance from 3% of the fauna in the Lower Stubensandstein to 25% in the Middle, and then apparently disappeared, while the other semi-aquatic predators, the phytosaurs, went from 41% in the Lower Stubensandstein to 30% in the Middle, 1% in the Upper, and 0% in the Knollenmergel. The shift from amphibian-dominated faunas in the Carnian to phytosaur-dominated faunas in the Norian, mixed phytosaur/dinosaur-dominated faunas in the midearly Norian, and dinosaur-dominated faunas in the later Norian probably corresponds to an environmental shift to drier conditions (Hunt 1991), but the shift was not a simple one-step control on the apparent composition of the faunas. The aquatic amphibians survived into the Middle Stubensandstein at least (and the Rhät, based on rolled specimens), and the phytosaurs into the upper Stubensandstein, and there was not a sharp Carnian/Norian disjunction produced by a change in the nature of fossil preservation.

The Carnian record in the Germanic basin is not complete enough to be sure what was going on before the Norian in detail. Latest Carnian faunas, from the Lehrbergschichten and Kieselsandstein (Table 1), seem to have been dominated by amphibians and phytosaurs. This is confirmed by the fauna of the Blasensandstein from Ebrach, Bavaria, equivalent in age to the Kieselsandstein, which has yielded four amphibian skulls (*Metoposaurus, Cyclotosaurus, Gerrothorax)* and remains of about ten phytosaurs (*Paleorhinus, Belodon;* Kuhn 1971,1983).

The Germanic sequence apparently documents the radiation of the dinosaurs, but does not clearly show the pre-dinosaur terrestrial faunas. The amphibian/phytosaur assemblages, presumably typical of freshwater/ terrestrial deposits, continue from the late Ladinian and Carnian into the early Norian. Their decline presumably has more to do with the preservation of changing facies, rather than being a direct ecological replacement.

It seems clear that the record in Germany does not show a simple switch from freshwater deposition to arid terrestrial deposition, corresponding to the faunal change, since conditions throughout the Carnian and Norian were largely arid. The Gipskeuper, Rote Wand, Lehrbergschichten, and Kieselsandstein (all presumably Carnian) show extensive evidence for arid desert-like conditions (Brenner 1979), and yet fossils are extremely rare, consisting only of rare lungfishes ( *Ceratodus)*, amphibians, and phytosaurs.

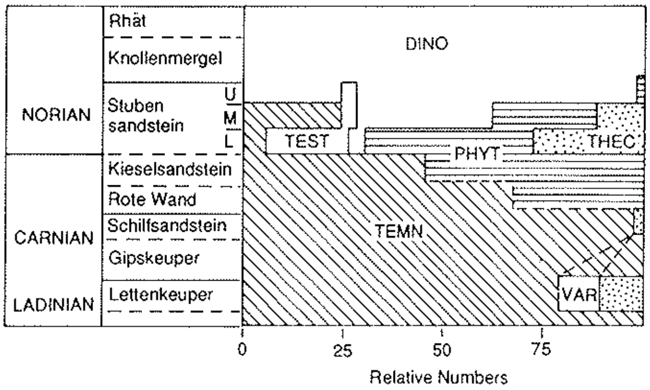


Fig. 9 - Faunal changes through the Late Triassic of south-western Germany, based on the data given in Table 1. Non-marine faunas are known from several levels in this sequence, but only those from the Lettenkeuper, Schilfsandstein, Stubensandstein (Unterer, Mittlerer, Oberer), and Knollenmergel were sufficiently diverse to provide percentage values. Temnospondyl amphibians and phytosaurs dominated earlier faunas, and the dinosaurs radiated rapidly in the Norian. Abbreviations: DINO, dinosaurs; PHYT, phytosaurs; TEMN, temnospondyl amphibians; TEST, testudinates; THEC, thecodontians other than phytosaurs; VAR, various (prolacertiforms, ? cynodonts). Modified from Benton (1986a).

## CONCLUSIONS

A case is made for the reality of the late Carnian extinction event both on land and in the sea. The criticisms of this event, that it is merely local in occurrence, or that it is the result of poor sampling of the fossil record, are countered. On land, the late Carnian extinction was much more significant than the end-Triassic one, in terms of the numbers of families that disappeared, the species-richness of those families at the time of disappearance, and the radiations that were enabled by the extinction.

There is value in undertaking global-scale analyses of these events in the Late Triassic, but also in studying local successions in order to achieve a detailed view of faunas against a more refined stratigraphy. Candidate successions that consist of terrestrial sediments spanning all or part of the Late Triassic and Early Jurassic are to be found in the Germanic Basin (the Keuper), the south-western United States (the Chinle Formation, Dockum Group, and others), eastern North America (the Newark Supergroup), Great Britain (the Lossiemouth Sandstone Formation and the fissure fills of the Bristol area and south Wales), Argentina (the Ischichuca, Ischigualasto, and Los Colorados Formations), India (the Maleri and Dharmaram Formations), southern Africa (the Elliot and Clarens Formations), and China (the Lower Lufeng Formation). At present, evidence from palynology, invertebrates, fishes, chronostratigraphy, and magnetostratigraphy helps to confirm the ages of units in some of the mentioned areas, but much more work is required in order to confirm stratigraphic schemes based mainly on tetrapod faunas.

A detailed example, from the Keuper sequence of south-western Germany, is given. This is based on extensive documentation of the finds from 75 localities and from eight differentiable geological formations spanning the late Ladinian to late Norian time interval. The results apparently show a rapid radiation of the dinosaurs during the Norian, following a presumed late Carnian extinction event. Unfortunately, this sequence is marred by a gradual change in faunal types from freshwater to arid terrestrial, and the earlier faunas of amphibians and phytosaurs are presumably not being replaced directly by the later faunas of dinosaurs.

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## DISCUSSION

J. F. BONAPARTE - Can you say anything about associated floral changes?

M. J. BENTON - Floral data are not so easy to determine on a global scale. However, the late Carnian tetrapod extinctions seem to correlate with the demise of the *Dicroidium* Floras of Gondwanaland, and its replacement by nothern-style conifer-dominated floras.

G. CUNY - Are all the extinction phenomena synchronous all around the world? Outcrops such as those of the French «Rhaetian» in which precise determination is impossible, will perhaps change some of your conclusions, because it is impossible to interpret such outcrops. For palynomorphs, it seems that there is no extinction event between the Norian and Hettangian.

M. J. BENTON - One cannot of course be sure of synchrony of these events globally. Even for the well-studied K-T event, synchrony is hard to determine. It is so much more difficult in the Triassic.

A. J. CHARIG - May I have your assurance that all the families alleged to have died out in your mass extinction events were monophyletic *sensu* Hennig? I realize that you may well have limited the scope of your talk because of the limitations of time, but you made no mention of any possible causal factors that would have produced the mass extinctions. In particular, when you say that the mid-Carnian effect was followed by a period of enhanced origination of new families, do you regard this as a replacement phenomenon or one in which the old families died out independently of the new ones and those new ones then radiated opportunistically?

M. J. BENTON - So far possible, all the families involved in this analysis are monophyletic. I did not address causes of the extinctions since I cannot offer any new evidence. The data clearly show that the ecologically dominant rhynchosaurs, dicynodonts, chiniquodonts, and others of the Carnian had disappeared before the radiations of dinosaurs - ceratosaurs and prosauropods - in the Norian. Hence, I can see no evidence for attempts to argue that the dinosaurs caused the extinction: the dinosaurs radiated opportunistically into a faunally depleted world. Tracking the expansions of dinosaur faunas through the Late Triassic, Hunt (1991) and others have found that dinosaurs were very rare in Carnian faunas (generally less than 1% of individuals), but expanded to considerable abundance in the early Norian (e.g. Upper Petrified Forest Member, Tecovas Formation, Unterer Stubensandstein) with rich deposits of *Coelophysis*, plateosaurs, and other dinosaurs.

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# APPENDIX

## LOCALITIES IN BADEN-WÜRTTEMBERG THAT HAVE YIELDED LATE TRIASSIC TERRESTRIAL TETRAPOD REMAINS

by M. J. Benton and R. Wild

The localities are listed according to the division of the 'Keuper' represented, and in order from the north-west to the south-east of the region (see Figures 6,7). The four-digit number following each locality name refers to the relevant sheet (Bl. = Blatt) number of the 1:25,000 scale Geologische Karte von Baden-Württemberg, published by the Landesvermessungsamt Baden-Württemberg. Map references are given, according to the German grid system, and were read by the author from high-scale topographic and geological maps of the area. In most cases, in the absence of precise locality information, a search was made on the maps for the term 'Stbr'. (= Steinbruch, i. e. quarry), or for other indications of exposure of Triassic sediments of the correct age close to the village or town named on the specimen label.

Taxa recorded from each locality are noted, together with estimates of numbers made from the major collections in the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Geologisch und Paläontologisches Institut der Universität, Tübingen (GPIT), the Bayerische Staatssammlung für Paläontologie und historische Geologie (BSPHG), and the Geologisch-Paläontologisches Institut und Museum der Georg-August-Universität, Göttingen (GPIG) in March/April 1982. The estimates of numbers of taxa are based on counts of skulls or whole skeletons, where possible, or of 'significant' specimens. For richer localities, estimates are based on minimum number of individuals (MNI) criteria: the minimum number of individual animals that could account for the known fossil remains. Generic names only are given, and these are based on label information; no attempt has been made to update the taxonomy in line with recent reviews. The taxa noted from the German Keuper are as follows:

Temnospondyl amphibians: *Cyclotosaurus, Gerrothorax, Hyperokynodon, Mastodonsaurus, Metoposaurus, Plagiosaurus, Plagiosternum, Plagiosuchus.*

Turtles: *Proganochelys, Proterochersis.*

Prolacertiform: *Tanystropheus.*

Choristodere: *Pachystropheus.*

Phytosaurs: *Belodon, Mystriosuchus, Nicrosaurus, Phytosaurus,* ?*Termatosaurus.*

Aetosaurs: *Aetosaurus, Dyoplax.*

Rauisuchians: *Teratosaurus, 'Thecodontosaurus', Ticinosuchus, Zanclodon.*

Crocodilomorph: *Saltoposuchus.*

Theropods: *Halticosaurus, Procompsognathus.*

Prosauropods: *Efraasia, Plateosaurus, Sellosaurus. 'Thecodontosaurus'.*

Nothosaur: *Nothosaurus.*

Ichthyosaur: *Ichthyosaurus.*

Cynodont: *Tricuspes.*

Mammals: *Microlestes, Thomasia, Triglyphus,* etc.

### Lettenkeuper

(1) Kupferzell (Bl. 6724/6824), Autobahn roadworks; 30,000 bones collected from a 200-300 mm thick greenish-yellow marl band (Wild 1978,1980). Fossils include ostracods, bivalves, hybodont sharks, 'chondrostean' fishes, lungfishes, *Gerrothorax* (?5), *Mastodonsaurus* (?30), cf *Cyclotosaurus* (2), the prolacertiform *Tanystropheus* (1), cf. *Ticinosuchus* (4), *Nothosaurus* (1), and cynodonts (?5) (SMNS).

(2) Michelbach/Bilz (Bl. 6924), *Mastodonsaurus* (1), *Plagiosuchus* (1), two new amphibians (2). Label reads «Bauaushub am nördlichen Ortsrand an der Strasse nach Hessental ... $^{35}$55725 $^{37}$37550 ... Obere Graue Mergel» (GPIT; SMNS).

(3) Schwäbisch Hall - Steinbach, near Hall (Bl. 7824), amphibians, nothosaurs, *Tanystropheus* (1), '*Teratosaurus*' (1) (SMNS).

(4) Bibersfeld, near Hall (Bl.7824), *Mastodonsaurus* (10), *Plagiosuchus* (2), '*Zanclodon*' (2), from the Lettenkeuper bonebed (GPIT, SMNS).

(5) Otterbach, near Hall (Bl. 7824), *Plagiosuchus* (1). Label reads «Talheim-Vellberg» (GPIT).

(6) Comburg, near Hall (Bl. 7824), *Mastodonosaurus* (2) (GPIT).

(7) Crailsheim (Bl. 6826), *Mastodonsaurus* (10), *Plagiosternum* (20), '*Thecodontosaurus*' (2) (BSPHG, GPIT).

(8) Gaildorf (Bl. 6924), *Mastodonsaurus* (3) from the Alaunschiefer, *Zanclodon* (1), *Nothosaurus* (1) (GPIG, GPIT, SMNS).

(9) Markgröningen, near Ludwigsburg (Bl. 7020), quarry in southern part of Rothenacker Wald (Fraas 1910, p. 19), *Mastodonsaurus* (1), lower to middle Lettenkeuper (SMNS).

(10) Ludwigsburg-Hoheneck and -Eglosheim (Bl. 7021), *Mastodonsaurus* (4), '*Zanclodon*' (1), *Psephosaurus* (1), *Simosaurus* (?5), *Nothosaurus* (?30) from the Lettenkeuper Dolomit (= Hohenecker Kalk) (Fraas 1910, pp. 19, 20) (GPIT, SMNS).

(11) Zuffenhausen, northern Stuttgart (Bl. 7120), *Mastodonsaurus* (2), *Plagiosuchus* (?5), '*Zanclodon*' (1), «an der Ziegelhütte bei Zuffenhausen» (Fraas 1910, p.19) (SMNS).

(12) Rottweil (Bl. 7817), *Plagiosuchus* (1). Brenner (1978b, p. 229) notes sections taken at $^{34}$74450 $^{53}$34750 and $^{34}$74550 $^{53}$35140 (GPIT).

### Schilfsandstein

(1) Heilbronn (Bl. 6821), Jägerhaussteinbruch, Wartenberg (large quarry at $^{35}$19375-$^{35}$19800/$^{54}$44125-$^{54}$44500; Wild 1968, p. 53), *Metoposaurus* (1), '*Hyperokynodon*' (1) (SMNS)

(2) Feuerbacher Heide (Bl. 7120/1; 7220/1), *Cyclotosaurus* (?30), *Metoposaurus* (?20-30), *Belodon* (1), *Dyoplax* (1), '*Thecodontosaurus*' (1) (Fraas 1910, p. 22). There are many old quarries between $^{35}$12250-$^{35}$12500/$^{54}$06625-$^{54}$06775. Ströbel and Wurm (1977, p. 42) note an exposure at $^{35}$114 $^{54}$059 (SMNS)

(3) Hanweiler (Bl. 7122), *Metoposaurus* (1). The old quarry in which the *Metoposaurus* skeleton was found ($^{35}$28525/$^{54}$13225-$^{54}$13400), still exists (R. Wild, pers. comm., 1992; see also Frank and Vollrath 1971, p. 47). Fraas (1896, p.8) noted that «Der Stein, in welchem wahrscheinlich das vollständige Skelet steckte, war seiner Zeit bereits behauen und geglättet, um als Gesimsstein an dem Bau des Postgebäudes verwendet zu werden», in other words, that the skeleton came from a shaped building stone used in construction of the Stuttgart post office.

(4) Wendelsheim (Bl. 7419), *Cyclotosaurus* (1). Outcrop of Schilfsandstein to the north-east, in old quarries around $^{34}$95600 $^{53}$75375 (GPIT).

### Obere Bunte Mergel (Lehrbergschichten)

(1) Sonnenberg (Bl. 7220/1), *Metoposaurus* (3), cf. *Plagiosternum* (1), *Belodon* (2), and the lungfish *Ptychoceratodus concinnus* (Plieninger) in the Rote Wand (Lang 1909, p. 113). Martin (1980) states that the outcrop is on Sonnenberg-Strasse, on the Bopser, a hill (about $^{35}$14500-$^{35}$14700/$^{54}$03175). This was a natural outcrop, enlarged by cuttings made to build houses (pers. comm. from O. Linck to R. Wild) (SMNS).

(2) Bopser, Stuttgart (Bl. 7221), *Cyclotosaurus* (1), *Metoposaurus* (1) (Thürach 1888, p. 114; Fraas 1910, pp. 22-23; Berckhemer 1939, p. XLV; Brenner 1978b, p. 222). Line of pits on north-western side of Wernhalde/Bopser, of which Berckhemer (1939, p. XV) notes $^{35}$13650 $^{54}$02900 as the source (SMNS).

### Kieselsandstein

(1) Botnang, Stuttgart (Bl. 7220), *Phytosaurus* (1). Old 'Stbr' at $^{35}$09425 $^{54}$06750; see Bräuhäuser and Frank (1932, p.20) (SMNS).

(2) Rettersberg, near Winnenden (Bl. 7122), rauisuchian (1), quarry c. 750 m NNE of Rettersberg ($^{35}$35300 $^{54}$16025).

### Unterer Stubensandstein

(1) Blindheim (Bl. 6823), quarry at $^{35}$46075 $^{54}$ 40250, '*Teratosaurus*' (1), *Proterochersis* (1) (SMNS).

(2) Ochsenbach (Bl. 6919), *Cyclotosaurus* (1), phytosaur (1), *Sellosaurus* (1). *Sellosarurus gracilis,* a plateosaur (Galton 1984) comes from beds 18-20 of Brenner (1978a, profile 8) at $^{34}$98500 $^{54}$31825, the *Cyclotosaurus* from a smaller quarry at $^{35}$97625 $^{54}$32000, the '*Ceratodus*-Bruch' of Linck, and the phytosaur skull from the large quarry at $^{35}$98375-$^{35}$98400/ $^{54}$32500-$^{54}$32175. See also Lang (1909, p. 129), Stoll (1929, p. 34), Brenner (1973, pp. 155-7, 1978b, pp. 215-6) (SMNS).

(3) Blankenhorn, near Güglingen (Bl. 6919), *Aetosaurus* (1). Found during «Wegebau SW Ruine Blankenhorn» (label), hence about $^{35}$99350 $^{54}$33625, at the horizon of the Ochsenbachschicht (Brenner 1973, p. 154), hence Lower Stubensandstein (Wild 1991) (SMNS).

(4) Löwenstein (Bl. 6922), phytosaur (?*Nicrosaurus*) (3). Locality probably old quarries at $^{35}$27175 $^{54}$39950. There are other quarries on the map at $^{35}$272 $^{54}$399, $^{35}$273 $^{54}$397, $^{35}$288 $^{54}$402, $^{35}$289 $^{54}$400, and $^{35}$293 $^{54}$392, and Brenner (1978b, p. 217) lists many sections for 'E. Löwenstein' ($^{35}$32000 $^{54}$39850). See also Brenner (1973, p. 183; 1978a, profile 1), Brenner and Villinger (1981, p. 64) (SMNS).

(5) Wüstenrot (Bl. 6922), Sandgrube am Chauseehaus bei Wüstenrot, an der Strasse von Löwenstein an Mainhardt, *Nicrosaurus* (1). ? Lower Stubensandstein at $^{35}$32950 $^{54}$39750.

(6) Murrhardt (Bl. 7023), Fleinssteinwerk Schlipf, *Proterochersis* (7), *Nicrosaurus* (2) (Brenner 1973, p. 157). Eisenhut (1971, p. 29; 1972, pp. 31-32) notes a quarry at $^{35}$414 $^{54}$257, and an older one at $^{35}$428 $^{54}$262. The locality Murrhardt/Köchersberg could be the quarry at $^{35}$441 $^{54}$259 (SMNS).

(7) Mettelberg, Murrhardt (Bl. 7023), *Proterochersis* (1). Large 'Stbr'. at $^{35}$46175 $^{54}$23425 (GPIT).

(8) Trailhof, near Oberbrüden (Bl.7023) old quarry at $^{35}$38575 $^{54}$25200, *Proterochersis* (1) (SMNS).

(9) Igelsbach, in the bed of this small stream, near Strasse Klaffenbach - Althütte (Bl. 7023), at about $^{35}$42100 $^{54}$18500, *Proterochersis* (1) (SMNS).

(10) Grunbach (Bl. 7122), *Proterochersis* (1). Lower Stubensandstein found by digging a hole for building a house in Grunbach in 1958, at about $^{35}$30750 $^{54}$09200 (SMNS).

(11) Kottweil, Sandwerk Heck (Bl.7122), *Nicrosaurus* (1). Locality at $^{35}$34150 $^{54}$12275.

(12) Rudersberg (Bl. 7123), *Proterochersis* (1). Eisenhut (1972, p. 32) quotes Fraas (1913, p.16) that the specimen comes from «dem Fleinsbruch am Kartenrand NW Rudersberg», hence $^{35}$36200 $^{54}$17450 (SMNS).

(13) Eselshalden, near Welzheim (Bl. 7123), *Proterochersis* (1). There are two quarries, and the fossil came from 'Stbr. rechts d. Strasse' (label), thus $^{35}$42675 $^{54}$13600, coming from the west. Brenner (1978b, p. 220) gives a section at $^{35}$42430 $^{54}$137000 (see also Villinger 1966, p. 67) (SMNS).

(14) Lorch (Bl. 7124), *Proterochersis* (1), '*Belodon*' (1). There is a quarry at $^{35}$51225 $^{54}$07725, and the *Proterochersis* came from the Beutental nearby (Bl. 7224) at about $^{35}$53 $^{54}$05. See also Brenner (1973, p. 157; 1978b, p. 221) (SMNS).

(15) Sindelfingen, Sandwerk Körner (Bl.7220), *Paratypothorax* (2), '*Belodon*' (8). Label says «3 km NNE Sindelfingen im Gewand Spitzholz», quarry marked at $^{35}$01075 $^{53}$99625 (SMNS).

(16) Stuttgart-Heslach (Bl. 7220), '*Belodon*' (20) rauisuchid (2), *Thecodontosaurus* (1), *Sellosaurus* (2). Fraas (1910, p. 23) notes that the site was below the Jägerhaus which was above a railway tunnel exit, at $^{35}$10400 $^{54}$02500 (Brenner 1978a, profiles 39-42). See also Brenner (1973, p. 171; 1978b, p. 222) and Gwinner and Hinkelbein (1976, pp. 79-80) (GPIT, SMNS).

(17) Kaltental (Bl. 7220), '*Teratosaurus*' (2), *Aetosaurus* (22). There was a large old quarry centred at $^{35}$105 $^{54}$007, which was the source for some finds by Kapff; it is now filled and the site of a Sportplatz. Ströbel and Wurm (1977) note that the large slab with *Aetosaurus* came from the Steinbruch in the Elsental at $^{35}$09760 $^{54}$00760 (see also Bach 1868, p. 13; Bräuhäuser and Frank 1932, p. 66; Brenner 1973, p. 171; Wild 1991) (SMNS).

(18) Stuttgart-Degerloch, Meistersingerstrasse (Bl.7220), *Nicrosaurus* (1). Locality at about $^{35}$12000 $^{54}$01750; specimen found during the building of a cellar.

(19) Gablenberg, Abelsberg Strasse (Bl. 7221), '*Belodon*' (1), Lower Stubensandstein here (about $^{35}$15700 $^{54}$05225) (SMNS).

(20) Rohracker (Bl. 7221), Fraas (1913) notes that the specimen came from a wine-maker from his vineyard. There is Lower Stubensandstein at $^{35}$17000 $^{54}$02350. See also Brenner 1973, p. 157; 1978b, p. 218) (SMNS).

(21) Engelberg, near Winterbach, Steinbruch von Frank (Bl. 7222), *Proterochersis* (1). Locality is marked 'Sgr.' at $^{35}$34125 $^{54}$05775 (see Frank 1965, p. 40; Frank and Vollrath 1971, p. 58; Brenner 1973, p. 157; 1978b, p. 223) (SMNS).

(22) Hüttenbachklinge, near Strümpfelbach (Bl. 7222), *Proterochersis* (1). Exact locality uncertain, about $^{35}$27800 $^{54}$05400 (SMNS).

(23) Reichenbach an der Fils (Bl. 7222), *Proterochersis* (1). Exact locality unknown, about $^{35}$33575 $^{53}$98275, an old quarry.

(24) Ebersbach an der Fils (Bl. 7223), *Postosuchus,* (1), *Sellosaurus* (1), from locality «b. Lutherlinde, Weg nach Büchenbronn; 400 m NNW von Kirche Ebersbach am Weg nach Schorndorf» (label), in a pit associated with the building of an old folks' home, hence $^{35}$38060 $^{53}$98235. See also Frank (1965, p. 34), Brenner (1973, p. 152; 1978b, p. 224), and Elsenhut (1975, p. 156) (SMNS).

(25) Häfnerneuhausen, Schönbuch (Bl. 7321), *Proganochelys* (1) [ = Neuenhaus]. Brenner (1978a, profile 74) gives a section in Kieselsandstein and Lower Stubensandstein from $^{35}$14500 $^{53}$88375 (GPIT).

(26) Lustnau, Tübingen (Bl. 7420), $^{35}$06 $^{53}$80, *Cyclotosaurus* (1), *Plagiosaurus* (1). Brenner (1978a, profile 97) gives a section at $^{35}$07000 $^{53}$80250, SE Bebenhausen, with Lower Stubensandstein, seemingly the nearest available locality with these older rocks (GPIT).

(27) Trossingen (Bl. 7917), Autobahn Stuttgart to Singen, west of Trossingen, found during construction, phytosaurs (3). Locality at about $^{34}$70000 $^{53}$27150 (SMNS).

### Mittlerer Stubensandstein

(1) Pfaffenhofen, Stromberg (Bl. 6919), Weisser or Burrerscher Steinbruch ($^{34}$975 $^{54}$338), *Cyclotosaurus* (5), *Gerrothorax* (3), '*Teratosaurus*' (2), *Aetosaurus* (4), *Mystriosuchus* (7), '*Phytosaurus*' (1), *Saltoposuchus* (5), *Procompsognathus* (2), *Halticosaurus* (4), 'theropod' (1), '*Efraasia*' (3), *Sellosaurus* (9), *Thecodontosaurus* (4), plateosaur (2). The dinosaurs occur in a brown/ grey sandstone (obere Faule) above a red/ green mudstone which lies on a white sandstone, the source of most of the other reptile remains. See Brenner (1978a, profile 6; 1978b, pp. 215-6) (SMNS).

(2) Magstadt, Sandwerk (Bl. 7219), *Cyclotosaurus* (24), '*Phytosaurus*' (4). 'Stbr.' at $^{35}$01200 $^{54}$00000; Schmidt (1928, pp. 33-34) mentions a nearby quarry on the Allmandswäldle (see also Stoll, 1929 and Brenner 1973, p. 172) (SMNS).

(3) Kayh (Bl. 7419), *Mystriosuchus* (4). Label says «es ist der Bruch *rechts* vom Weg, wenn man von Kayh kommt...Bruch am Schönbuchrand», corresponding to a 'Stbr.' marked at $^{34}$942 $^{54}$828. Schmidt (1928, p. 30) notes that Quenstedt referred to dinosaurs from the 'Ammertal', referring to the river Ammer on which Kayh lies. See also Bräuhäuser and Frank (1932, p. 67) and Brenner (1978a, profile 77; 1978b, p. 226) (GPIT, SMNS).

(4) Neuhaus, near Aixheim (Bl. 7818), *Proganochelys* (3), *Mystriosuchus* (20), '*Teratosaurus*' (6), *Plateosaurus* (3). 'Stbr.' on old map at $^{34}$77100 $^{53}$30400, and smaller one at $^{34}$772 $^{53}$303, of which Berz (1933, p. 14) says the source was probably the first. Berz (1936, p. 18) refers to fossils «in den Steinbruchen beim Neuhaus...». Lang (1909, p. 99) and Brenner (1978b, p. 230) give a section at $^{34}$77359 $^{53}$30300, which is not the tetrapod locality. See also Lang (1909, p. 101), Bräuhäuser and Frank (1932, p. 66), Brenner (1973, p. 171; 1978a, p. 179), Villinger (1973, p. 216), and Brenner and Villinger (1981, p. 55) Includes '*Teratosaurus*' from 'Aldingen' (GPIT, SMNS).

(5) Schwenningen (Bl. 7917), $^{34}$65 $^{53}$25, '*Teratosaurus*' (1), *Plateosaurus* (1). Exact locality uncertain; Brenner (1978b, p. 230) notes a section by Stoll (1929, p. 26) at $^{35}$670 $^{53}$235. Schmidt (1914, p. 31) notes quarries «im Walde nordöstlich der Bezeichnung 'Wannengrund'» on the map (GPIT, SMNS).

(6) Untere Mühle, Trossingen (Bl. 7917), $^{34}$750 $^{53}$279, '*Belodon*' (1), *Mystriosuchus* (1), '*Teratosaurus*' (3), *Sellosaurus* (2), plateosaur (2). Schmidt (1914, pp. 31, 112) notes a quarry below the Untere Mühle ($^{34}$750 $^{53}$279) with Stubensandstein reptiles, close to the famous Knollenmergel site (q.v.) (GPIT).

### Oberer Stubensandstein

(1) Häfnerhaslach, Stromberg (Bl. 6919), exact locality uncertain ($^{35}$94 $^{54}$32), *Plateosaurus* (1), Lower to Upper Stubensandstein here? See also Linck (1969, p. 48), Brenner (1973, pp. 183-4) (SMNS).

(2) Stromberghöhe, Markung Zaberfeld (Bl. 6919), *Plateosaurus* (1). Locality in the highest part of the Stubensandstein, at about $^{34}$95200 $^{54}$32900.

(3) Rübgarten, Wildenau (Bl. 7421), *'Phytosaurus'* (1). Bach (1868, p. 13) states locality lies «Südlich von Ruine Wildenau am unteren Dürrenberg», hence $^{35}$125 $^{53}$793, which is labelled 'Ehem. Burg Wildenau' on the map. See also Bräuhäuser and Frank (1932, p. 66) and Brenner (1978b, p. 21) (GPIT, SMNS).

(4) Trossingen, Obere Mühle (Bl. 7917), *Proganochelys* (3), *Plateosaurus* (?60). Site of the famous *Plateosaurus* digs in 1911-2 (Stuttgart), 1921-3 (Tübingen), and 1932 (Stuttgart). Schmidt (1914, pp. 32-33) describes the same locality, while Huene (1923) and Seemann (1933) gave sections at $^{34}$74200 $^{53}$27125 for an excavation pit in the Knollenmergel, now belonging to the Upper Stubensandstein (Brenner 1973, p. 171; 1978a, profiles 114-5; 1978b, p. 230; Brenner and Villinger 1981, p. 55). Berz (1933, pp. 15-16) incorrectly indicates that they were found «im Trosseltal unmittelbar unterhalb der oberen Mühle» (SMNS).

### Knollenmergel

(1) Wüstenrot (Bl. 6922), $^{35}$34 $^{54}$38, *Plateosaurus* (1). Exact locality uncertain; several quarries with Knollenmergel around the town; label reads «5 m unter der Psilonoten Bank» (GPIT).

(2) Treubendorf (Bl. 7123), *Plateosaurus* (1). «Westabhang zwischen Treubendorf und Langenberg, bei Welzheim bei Gmünd», around $^{35}$44 $^{54}$16 (GPIT).

(3) Degerloch (Bl. 7220), *Plateosaurus* (5). One *Plateosaurus* specimen was found during excavation of an air-raid shelter in 1945, and the others in two pits dug for marl to improve the soil in nearby vineyards, on the Weinberge, near Degerloch ($^{35}$11050 $^{54}$01370). See also Fraas (1910, p. 24); Bräuhäuser and Frank (1932, p. 75), Ströbel and Wurm (1977, p. 56), Brenner (1973, p. 191, 1978a, profile 45; 1978b, p. 222) (SMNS).

(4) Erlenberg (Bl. 7220), *Plateosaurus* (3). Ströbel and Wurm (1977, p. 56) give the source as a railway cutting at $^{35}$08540 $^{54}$00850, and 10 m below the Lias boundary (SMNS).

(5) Schönaich, near Böblingen (Bl. 7320), *Plateosaurus* (1). Label says «Am Hang Schönaicher Forst in 8 m Tiefe beim Brunnengraben gefunden», hence near the Bahnhof where two old railway lines split NW of Schönaich at about $^{35}$03 $^{53}$92. The specimen was found during excavations to build a fountain (SMNS).

(6) Bebenhausen, near Tübingen (Bl. 7420), $^{35}$04 $^{54}$80, *Plateosaurus* (1). Exact locality uncertain; fossils noted from Rothen Graben, near Bebenhausen, and Knollenmergel occurs all round that town (GPIT).

(7) Brandklinge, near Tübingen-Pfrondorf (Bl. 7420), *Plateosaurus* (1). Stream in deep valley from $^{35}$083 $^{53}$800 to $^{35}$091 $^{53}$788 lies in Knollenmergel (GPIT).

(8) Jächklinge, near Tübingen (Bl. 7420), *Plateosaurus* (1). The name Jächklinge does not appear on the map; F. Westphal (pers. comm.) suggests possibly Gähklinge ($^{35}$084 $^{53}$796) which lies in Knollenmergel (GPIT).

(9) Pfrondorf, near Tübingen (Bl. 7420), *Plateosaurus* (?6). May be the same as previous locality (GPIT).

(10) Ostdorf, near Balingen (Bl. 7619), *Plateosaurus* (1). The specimen was found in 1906; the exact locality is not known, but perhaps lay on the river Eyach. See Brenner (1973, p. 191) (SMNS).

(11) Sunthausen, Donaueschingen (Bl. 7917), *Plateosaurus* (c.5) The bones (about 50 elements) were found in one layer at the base of the Knollenmergel during the building of the Autobahn from Bad Durrheim to Donaueschingen at about $^{34}$66050 $^{53}$17375 (SMNS).

(12) Waldshut (Bl. 8315), $^{35}$34 $^{54}$38, *Plateosaurus* (1). Label says «Gemeindwald Fützen, Kreis Waldshut - Grenze km5/km4?» (GPIT).

### Rhätsandstein

(1) Sonnenberg, near Möhringen (Bl. 7220), *Termatosaurus,* archosaur. Labels read «im Gräsert» and «im Kressert.» (SMNS).

(2) Stuttgart-Degerloch (Bl. 7220), *Termatosaurus, Belodon* (reworked tooth, 1), *'Pachystropheus'*, *Ichthyosaurus.* Includes Bopserwald, Degerloch (SMNS).

(3) Rüdern, near Esslingen (Bl. 7221), *Termatosaurus* (SMNS).

(4) Birkengehren, near Esslingen (Bl. 7221) *Termatosaurus.*

(5) Nellingen (Bl. 7221), *Termatosaurus,* (SMNS).

(6) Steinenbronn (Bl. 7320), *Termatosaurus* (SMNS).

(7) Schlösslesmühle, near Echterdingen (Bl. 7320/1), amphibian, *Termatosaurus* (2), turtle, plateosaur tooth (SMNS).

(8) Nörtingen/ Steinenberg (Bl. 7322) turtle (SMNS).

(9) Lustnau, Hägnach, Tübingen (Bl. 7420), turtle (1), *Plateosaurus* (1). 'Stbr.' in Rät at Hägnach ($^{35}$061 $^{53}$791), or nearby (GPIT, BSPHG).

(10) Bebenhausen, Olgahain (Bl. 7420), Rhät bonebed with bones of amphibians and reptiles, including phytosaurs (teeth, 3), turtle (plastron fragment, 1), cynodonts, and tritheledonts, and teeth of *Tricuspes, Triglyphus. Microlestes,* etc. (GPIT).

(11) Tübingen, *Termatosaurus, Belodon* (SMNS).

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