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Global Triassic tetrapod biostratigraphy and biochronology

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Abstract

Eight, temporally successive assemblage zones of tetrapod fossils provide the basis for dividing Triassic time into eight land-vertebrate faunachrons. These land-vertebrate faunachrons, their type assemblage zones, and their approximate correlation to the standard global chronostratigraphic scale are (ascending order): (1) Lootsbergian (*Lystrosaurus* Assemblage Zone, Balfour, Katberg and Burgersdorp formations, Karoo basin, South Africa) = late Dorashamian–Induan; (2) Nonesian (*Cynognathus* Assemblage Zone, Burgersdorp Formation, Karoo basin, South Africa) = Olenikian; (3) Perovkan (*Shansiodon* Assemblage Zone, Donguz Formation, Russian Urals) = Anisian; (4) Berdyankian (*Mastodonsaurus* Assemblage Zone, Bukobay Formation, Russian Urals) = Ladinian–early Carnian; (5) Otischalkian (*Paleorhinus* Assemblage Zone, Chinle Group, Chinle basin, USA) = late-early to early-late Carnian; (6) Adamanian (*Rutiodon* Assemblage Zone, Chinle Group, Chinle basin, USA) = latest Carnian; (7) Revueltian (*Pseudopalatus* Assemblage Zone, Chinle Group, Chinle basin, USA) = Norian; (8) Apachean (*Redondasaurus* Assemblage Zone, Chinle Group, Chinle basin, USA), = Rhaetian. The Triassic land-vertebrate faunachrons provide a framework for the correlation of Triassic nonmarine deposits with a temporal resolution comparable to the seven Triassic Stage/Ages of the standard global chronostratigraphic scale.

Keywords: Triassic; biostratigraphy; faunachrons; biochronology; tetrapod

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1. Introduction

Fossil vertebrates, especially tetrapods, have long been used to correlate nonmarine Triassic strata (e.g., Ochev and Shishkin, 1989; Lucas, 1990). This use dates back at least as far as Huxley (1869), who used rhynchosaurs to correlate Triassic strata in India and the United Kingdom. Here, I present a comprehensive tetrapod biostratigraphy and biochronology for the Triassic strata of Pangaea (Fig. 1). To do so, I define, or redefine, Triassic land-vertebrate faunachrons, which are eight time intervals equivalent to successive assemblage zones of Triassic tetrapod fossils.

2. Vertebrate biochronology

Wood et al. (1941) introduced the term land-mammal 'age' (LMA) to refer to intervals of Cenozoic time characterized by distinctive mammalian fossil assemblages from western North America. LMAs have been defined to encompass Cenozoic time intervals on most of the world's continents (Savage and Russell, 1983). For the Mesozoic, LMAs have

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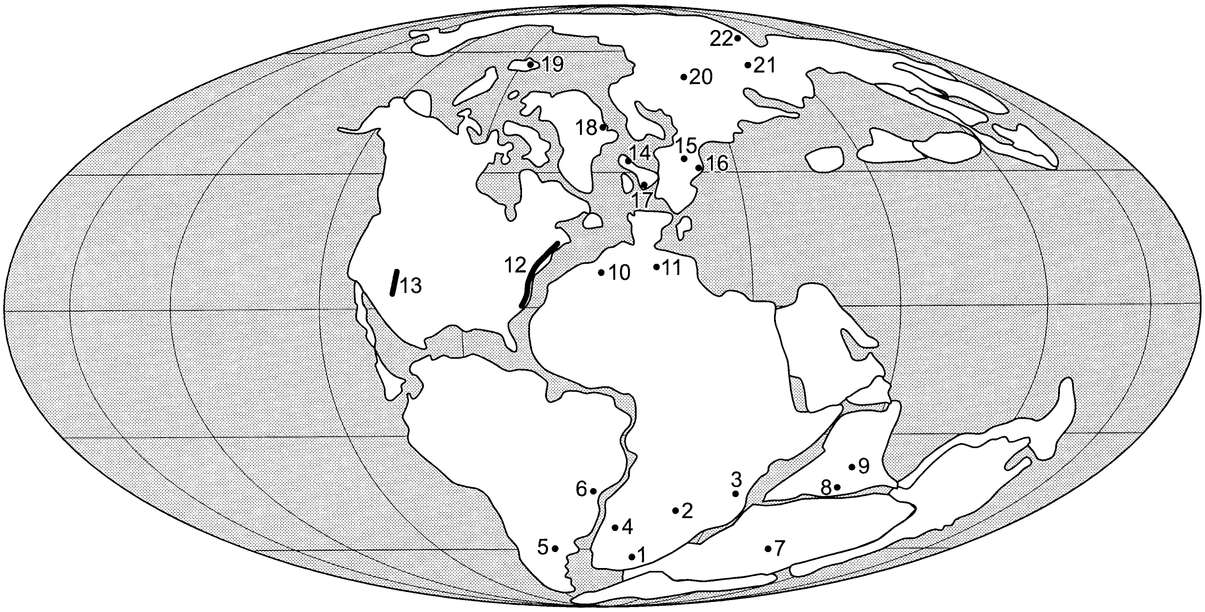

Fig. 1. Map of Triassic Pangaea showing locations of principal vertebrate fossil assemblages correlated in this article. Locations are: *1* = Karoo basin, South Africa; *2* = Zambia; *3* = Tanzania; *4* = Namibia; *5* = Argentina; *6* = Brazil; *7* = Transantarctic Mountains, Antarctica; *8* = Pranhita–Godavari Valley, India; *9* = Damodar, India; *10* = Essaouira basin, Morocco; *11* = Ilizi basin, Algeria; *12* = Newark Supergroup basins, eastern USA–Canada; *13* = Moenkopi and Chinle basins, western USA; *14* = Scotland; *15* = Germanic basins; *16* = northern Italy; *17* = Devon, United Kingdom; *18* = eastern Greenland; *19* = Svalbard; *20* = Russian Urals; *21* = Junggur basin, China; *22* = Ordos basin, China.

been proposed for the Late Cretaceous of western North America. However, more broadly based land-vertebrate 'ages' (LVA) or land-vertebrate faunachrons (LVF) have been introduced for parts of the Mesozoic record of Asia, South America and North America. Thus, LVAs or LVFs have been proposed for the Triassic of China (Lucas, 1993a) and Argentina (Bonaparte, 1966), the Late Triassic of western (Lucas and Hunt, 1993b) and eastern North America (Huber et al., 1993a), the Late Jurassic–Early Cretaceous of western North America (Lucas, 1993d), and the Late Jurassic–Cretaceous of Mongolia (Jerzykiewicz and Russell, 1991). Russell (1993) proposed marine vertebrate ages for the Cretaceous of western North America.

An aggregation of vertebrate fossils that has some stratigraphic range in a body of sedimentary rock (strata) is an assemblage zone. Vertebrate paleontologists have long referred to such an assemblage zone as a fauna or local fauna. The geologic time equivalent to a mammalian fauna is a LMA. This means that LMAs are biochronological units, intervals of geologic time recognized by distinctive fossils (Tedford, 1970).

LMAs are not the ages of formal stratigraphic terminology. Such ages are intervals of geologic time equivalent to stages, which are bodies of strata. Each age is thus based directly on strata in a specific area; these strata are the stratotype of the stage-age. However, LMAs lack such stratotypes, so to call them ages is to use that term in a different sense than is usual, which is why the term 'age' is usually placed in quotation marks.

Mammals are not the only vertebrates that can be used to recognize intervals of geologic time. In the Mesozoic, especially prior to the Late Cretaceous, when mammals are very rare as fossils, non-mammalian tetrapods can be biochronologically useful. For this reason, some workers use the term land-vertebrate 'age'. Because LMAs and LVAs are not formal ages in stratigraphy, Lucas (1993a) introduced the term faunachron (essentially the same concept as 'faunichron' of Dunbar and Rodgers (1957)) to refer to the time equivalent to the duration of a fauna.

He argued that the more precise term land-vertebrate faunachron (LVF) should replace LMA and LVA.

To define an LVF, a distinctive assemblage of vertebrate fossils must be identified. The name of the LVF is a geographic name taken from the place where (or very close to where) the vertebrate fossils were collected. Most previously proposed LMA and LVA names have been taken from the rock formation in which the fossils are found. The rock formation name is based on a place name. However, using the rock formation name can cause confusion because it may imply that the LMA or LVA refers to the duration of deposition of the formation, not just to the duration of the vertebrate fossil assemblage, which is often much shorter. It is less confusing to choose another place name for the LMA or LVA. For example, the Late Triassic Ischigualastian LVA of Argentina (Bonaparte, 1966) is named for the Ischigualasto Formation, although the Ischigualastian vertebrates do not occur throughout the Ischigualasto Formation. In contrast, the Late Triassic Adamanian LVF of western North America (Lucas and Hunt, 1993a) is named after Adamana, where the fossils occur, not after the Petrified Forest Formation, which contains the fossils.

LVFs are biochronological units, and I define their beginnings by biochronological events. Each LVF begins with the FAD (first appearance datum) of a tetrapod index genus. In so doing, the end of an LVF is defined by the beginning of the succeeding LVF, which is the FAD of another tetrapod index genus. This is a precise way to define LVF boundaries. They are, in effect, interval (assemblage) biochrons. It also provides the flexibility to define new LVFs by identifying an FAD within an existing LVF as the beginning of the new LVF.

The type tetrapod assemblage is the primary basis for characterization of the LVF, and its taxa are listed at the genus and species level. Index fossils identified here meet the criteria of true index fossils (temporally restricted, common, widespread, easily identified) and do not include rare taxa that happen to be restricted to an LVF, usually as single records.

This article does not comprehensively correlate all Triassic tetrapod assemblages. Only principal correlatives of the type assemblage of each LVF are listed. These are tetrapod assemblages that are reasonably well studied, diverse and for which the correlation is clear. I make a strong effort to cross-correlate the LVFs to the standard global chronostratigraphic scale (SGCS). However, the tetrapod biochronology of the Triassic proposed here is a time scale independent of the SGCS.

3. Previous vertebrate-based subdivisions of Triassic time

Although tetrapods have long been used to correlate nonmarine Triassic strata, relatively few efforts have been made to establish a formal tetrapod biostratigraphy or biochronology of the global Triassic (Fig. 2). The earliest, and perhaps most influential, Triassic tetrapod biostratigraphy was introduced by Broom (1906, 1907, 1909) for the Lower Triassic of the Karoo basin in South Africa. Broom identified three successive biostratigraphic intervals, the *Lystrosaurus*, *Procolophon* and *Cynognathus* ‘beds’. Watson (1914a,b) later termed these ‘zones’, and since Kitching (1970), the *Lystrosaurus* and *Procolophon* zones have been combined into a single, *Lystrosaurus* zone. Identification of the *Lystrosaurus* and/or *Cynognathus* ‘beds’ or ‘zones’ has long been possible in Antarctica, South America, India, China and Russia because of the cosmopolitanism of Early Triassic tetrapods, especially the genera *Lystrosaurus* and *Cynognathus*.

Romer (1975) (also see Cox, 1973) presented the first global Triassic tetrapod biochronology when he identified three successive types of land-vertebrate ‘faunas’: A (Early Triassic), B (Middle Triassic) and C (Late Triassic) (Fig. 2). Cosgriff (1984) divided Romer’s division A into A1 (= *Lystrosaurus* biochron) and A2 (*Cynognathus* biochron). Ochev and Shishkin (1989) (also see Anderson and Cruickshank, 1978) recognized the same intervals as Romer, but chose to name them the proterosuchian epoch (= A), kannemeyerioidean epoch (= B) and dinosaurian epoch (= C).

Cooper (1982) proposed a more detailed global tetrapod biostratigraphy of the Triassic than did Romer (Fig. 2). He recognized a succession of six Triassic zones based largely on a perceived stratigraphic succession of dicynodonts (see Lucas and Wild, 1995 for a revised dicynodont biozonation). Note that Cooper (1982) considered the *Lystrosaurus*

<table>
<tr><th colspan="2">PERIOD</th><th>Bonaparte (1966) [Argentina]</th><th>Romer (1975)</th><th>Cooper (1982)</th><th>Ochev & Shishkin (1989)</th><th>Lucas (1993) [China]</th><th>Lucas & Hunt (1993b) [W. USA]</th><th>Huber et al. (1993b) [E. N. AM.]</th></tr>
<tr><td rowspan="16">TRIASSIC</td><td rowspan="8">LATE</td><td rowspan="3">▨</td><td rowspan="8">C</td><td rowspan="3">*Plateosaurus* zone</td><td rowspan="8">dinosaurian epoch</td><td rowspan="10">▨</td><td>Apachean LVF</td><td rowspan="2">Cliftonian LVF</td></tr>
<tr><td rowspan="3">Revueltian LVF</td></tr>
<tr><td rowspan="2">Neshanician LVF</td></tr>
<tr><td rowspan="2">Coloradian</td><td rowspan="4">*Placerias* zone</td></tr>
<tr><td rowspan="2">Adamanian LVF</td><td rowspan="2">Conewagian LVF</td></tr>
<tr><td rowspan="3">Ischigualastian</td></tr>
<tr><td rowspan="2">Otischalkian LVF</td><td rowspan="2">Sanfordian LVF</td></tr>
<tr><td rowspan="2">*Stahleckeria* zone</td></tr>
<tr><td rowspan="4">MIDDLE</td><td rowspan="3">Chanarian</td><td rowspan="4">B</td><td rowspan="4">kannemeyeroidean epoch</td><td rowspan="8">▨</td><td rowspan="2">▨</td></tr>
<tr><td>*Dinodontosaurus* zone</td></tr>
<tr><td rowspan="2">*Tetragonias* zone</td><td rowspan="2">Ningwuan LVF</td><td rowspan="2">Economian LVF</td></tr>
<tr><td>▨</td></tr>
<tr><td rowspan="4">EARLY</td><td rowspan="2">Puestoviejan</td><td rowspan="4">A</td><td rowspan="4">*Kannemeyeria* zone</td><td rowspan="4">proterosuchian epoch</td><td>Ordosian LVF</td><td rowspan="4">▨</td></tr>
<tr><td>Fuguan LVF</td></tr>
<tr><td rowspan="2">▨</td><td>▨</td></tr>
<tr><td>Jimsarian LVF</td></tr>
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Fig. 2. Previously proposed Triassic tetrapod biochronologies and biostratigraphies.

zone to be Permian. However, Cooper's zonation has not been used by subsequent workers. The status of global Triassic tetrapod biostratigraphy and biochronology thus has not progressed much beyond that of Romer (1975), as the most recently published synthesis (Ochev and Shishkin, 1989) indicates.

More detailed subdivision of Triassic time has been made in provincial biochronologies proposed for Argentina, North America and China. Bonaparte (1966, 1967, 1982) introduced a set of 'provincial ages' for the Triassic of Argentina, but he never defined these terms (Fig. 2). (Lucas and Harris, 1996, did define the Chanarian as an LVF.) Lucas (1993a) proposed a succession of LVFs for the Chinese Early–Middle Triassic tetrapod record. Lucas and Hunt (1993b) proposed Late Triassic LVFs based on the Chinle Group tetrapod record from the western United States, and Huber et al. (1993b) proposed Middle–Late Triassic LVFs based on the Newark Supergroup record of eastern North America (Fig. 2).

Lucas and Huber (1998) reviewed global Late Triassic tetrapod biochronology and demonstrated the broad utility of the Chinle Group tetrapod biochronology proposed by Lucas and Hunt (1993b; also see Lucas, 1997). The status of 'provincial' tetrapod biochronology of the Triassic is that schemes exist for the Argentinian and Chinese record and for the Middle–Late Triassic record from North America. Although I propose here a global tetrapod biochronology, this does not obviate the need for some provincial biochronologies, whose utility as a secondary standard (Cope, 1996) is discussed below.

4. Lootsbergian LVF

4.1. *Definition*

I propose the term Lootsbergian LVF to refer to the time equivalent to the *Lystrosaurus* Assemblage Zone in the Balfour (Palingkloof Member), Katberg and Burgersdorp (lower part) formations of the Karoo basin of South Africa (Groenewald and Kitching, 1995). This assemblage zone encompasses a section up to 830 m thick (Fig. 3), with a type locality designated by Groenewald and Kitching (1995) around Lootsberg Pass. Lootsbergian time begins with the FAD of *Lystrosaurus*. The end of the Lootsbergian is equivalent to the beginning of the Nonesian, which is defined by the FAD of *Cynognathus*.

Broom (1906) introduced two successive zones — *Lystrosaurus* and *Procolophon* — that Kitching (1970, 1977) later combined into a single, *Lystrosaurus* Zone. Keyser (1979) referred to this same zone as the *Lystrosaurus–Thrinaxodon* Assemblage Zone. The original name *Lystrosaurus* Zone (or Assemblage Zone) is again in use (Groenewald and Kitching, 1995).

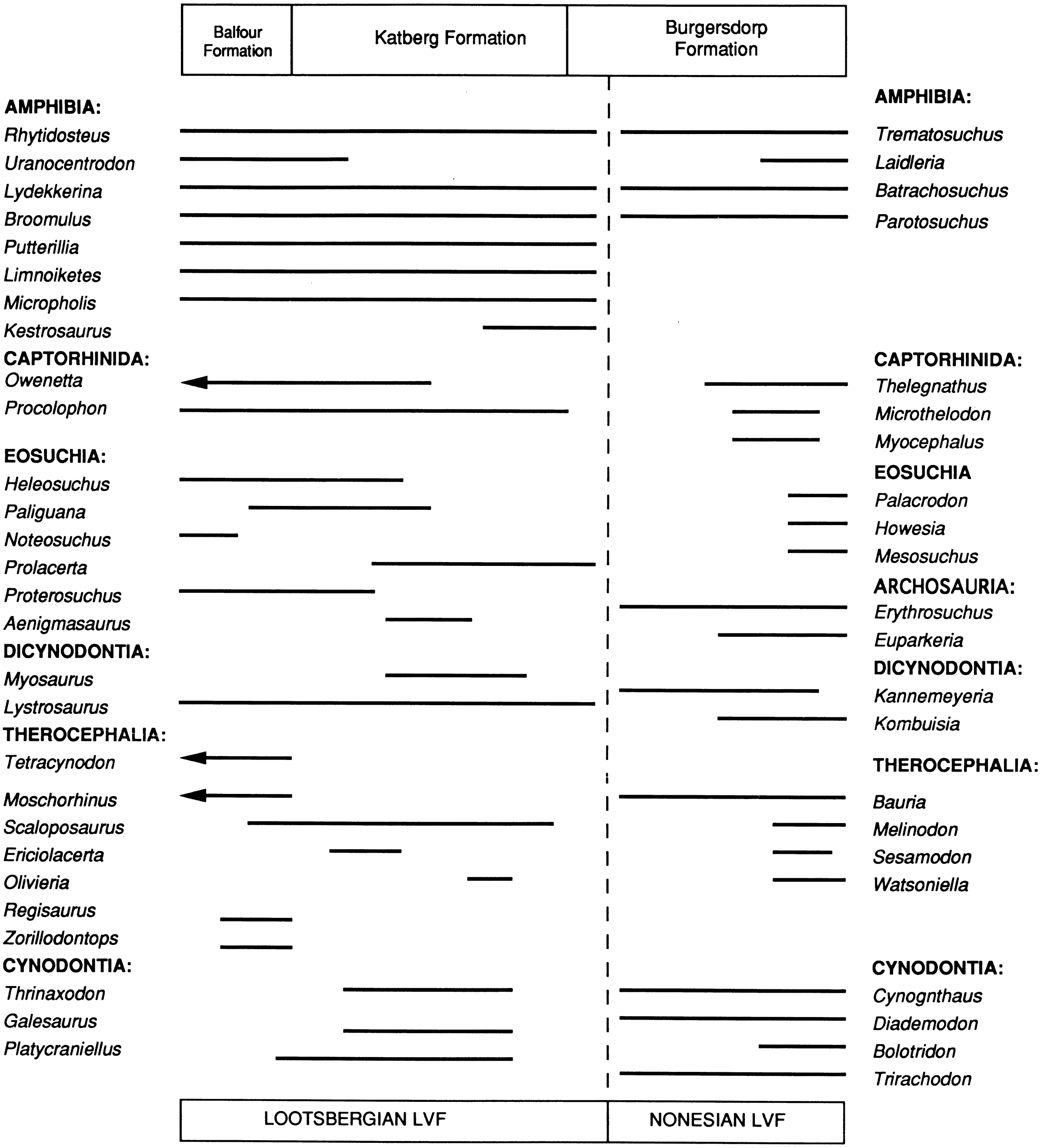


Fig. 3. Stratigraphic distribution of land vertebrates of the Lootsbergian and Nonesian LVFs in the Karoo basin of South Africa (after Groenewald and Kitching, 1995; Kitching, 1995).

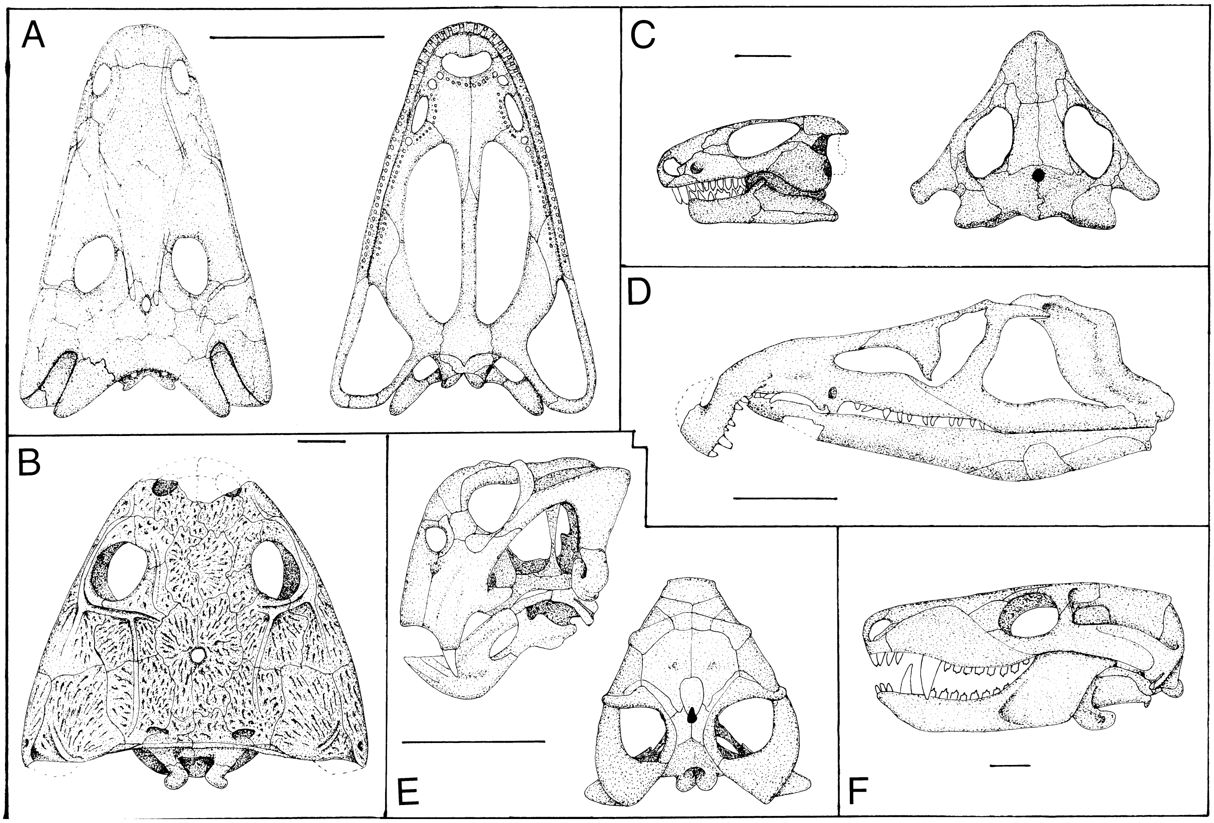


Fig. 4. Some Lootsbergian index fossils. (A) *Wetlugasaurus* skull, dorsal (left) and ventral (right) views. (B) *Tupilakosaurus*, dorsal view of skull. (C) *Procolophon*, lateral (left) and dorsal (right) views of skull. (D) *Proterosuchus* (= *Chasmatosaurus*), lateral view of skull. (E) *Lystrosaurus*, lateral (left) and dorsal (right) views of skull. (F) *Thrinaxodon*, lateral view of skull and lower jaw. (A, B) After Shishkin; (C, E) after Kitching; (D) after Young; (F) after Hopson. Bar scales: (A, D, E) 10 cm long; (B, C) 10 mm long.

4.2. Index fossils

The following tetrapod genera are restricted to Lootsbergian time and are widespread and/or common enough to be useful as index fossils: *Wetlugasaurus*, *Tupilakosaurus*, *Luzocephalus*, *Lydekkerina*, *Procolophon*, *Lystrosaurus*, *Scaloposaurus*, *Thrinaxodon*, *Proterosuchus* (= *Chasmatosaurus*) and *Prolacerta* (Fig. 4).

4.3. Type vertebrate fossil assemblage

The type assemblage of the Lootsbergian LVF is the *Lystrosaurus* Assemblage Zone of the Karoo basin, South Africa. The following taxa are present: the temnospondyls *Broomulus dutoiti* (Broom), *Kestrosaurus dreyeri* Haughton, *Pneumatostega potamia* Cosgriff and Zawiskie, *Limnoiketes paludinatans* Parrington, *Lydekkerina huxleyi* (Lydekker), *Micropholis stowi* Huxley, *Putterillia platyceps* Broom, *Rhytidosteus capensis* Owen and *Uranocentrodon senekalensis* (van Hoepen) (note that Cosgriff, 1984, suggested *Broomulus* and *Putterillia* to be synonyms of *Lydekkerina*); the captorhinids *Owenetta* sp. and *Procolophon trigoniceps* Owen; the eosuchians *Heleosuchus griesbachi* (Owen), *Paliguana whitei* Broom, *Noteosuchus colletti* (Watson), *Aenigmasaurus grallator* Parrington and *Prolacerta broomi* Parrington; the archosaurs *Proterosuchus fergusi* Broom, *P. vanhoepeni* (Haughton); the dicynodonts *Lystrosaurus oviceps* Haughton, *L. curvatus* (Owen), *L. declivis* (Owen), *L. murrayi* (Huxley), *L. maccaigi* (Seeley) and *Myosaurus gracilis* Haughton; the therocephalians *Ericiolacerta parva* Watson, *Moschorhinus kitchingi* Broom, *Oliviera parringtoni* Brink, *Regisaurus jacobi* Mendrez, *Scaloposaurus constrictus* Owen, *Tetracynodon darti* Sigogneau and *Zorillodontops gracilis* Cluver; and the cynodonts *Galesaurus planiceps* Owen, *Platycraniellus elegans* (van Hoepen) and *Thrinaxodon liorhinus* Seeley.

Kitching (1977) reviewed the *Lystrosaurus* Assemblage Zone localities, and Groenewald and Kitching (1995) provided a recent synopsis of the stratigraphic ranges of these genera, which is incorporated into Fig. 3. The *Lystrosaurus* Assemblage Zone has long provided a standard for correlation of the oldest Triassic tetrapod assemblages, so it logically serves as the basis for the oldest Triassic LVF (though it encompasses the Permo–Triassic boundary). In general, the *Lystrosaurus* Assemblage Zone produces a relatively low-diversity assemblage of reptiles, in which *Lystrosaurus* is abundant and associated with *Procolophon*.

4.4. Principal correlatives

The terms *Lystrosaurus* zone, beds or fauna have been applied to a wide geographic range of strata/fossils of Lootsbergian age. Most significant correlatives are the vertebrate fossil assemblages of the following locations: the upper Guodikeng and lower Jiucaiyuan formations, Junggur basin, China; the Heshanggou Formation, Ordos basin, China; the lower part of the Fremouw Formation, Antarctica; the Panchet Formation, India; the Vokhmian horizon of the Vetluga Series, Russian Urals; and the Wordy Creek Formation, eastern Greenland. Note that the supposed *Lystrosaurus* record from Laos (Repelin, 1923; Piveteau, 1938) is now known to be of the Late Permian dicynodont *Dicynodon* (Battail et al., 1995).

In northwestern China, land-vertebrates of Lootsbergian age come from the upper part of the Guodikeng Formation and the lowermost Jiucaiyuan Formation (both Cangfanggou Group) near Jimsar northeast of Urumqi (Pinyin: Wulumuqi) in western Xinjiang. These vertebrates are the '*Lystrosaurus* fauna' of northwestern China of some workers (e.g., Sun, 1972) and they provided the basis of the Jimsarian LVF of Lucas (1993a). Taxa present are the prolacertid protorosaur *Prolacertoides jimusarensis* Young, the procolophonid? *Santaisaurus yuani* Koh, the proterosuchian *Proterosuchus* (= *Chasmatosaurus*) *yuani* Young, the regisaurid therocephalian *Urumchia lii* Young, and the dicynodont *Lystrosaurus*, of which seven species have been named, some of which are not valid (see Colbert, 1974): *L. youngi* Sun, (= *L. curvatus*: Colbert, 1974), *L. weidenreichi* Young (a *nomen dubium* based on postcrania), *L. robustus* Sun, *L. latifrons* Sun, *L. hedini* Young, *L. broomi* Yuan and Young (= *L. murrayi*: Colbert, 1974), and *L. shichanggouensis* Cheng.

In the Ordos basin of north-central China, near Fugu, Shanxi, the upper part of the Heshanggou Formation produces a vertebrate fauna that was the basis of the Fuguan LVF of Lucas (1993a). Taxa present are indeterminate capitosauroids, the procolophonids *Eumetabolodon bathycephalus* Li and *E. dongshengensis* Li, the erythrosuchid *Fugusuchus hejiapensis* Cheng and the ordosiid therocephalian *Hazhenia concava* Sun and Hou. This and a correlative assemblage from the Junggur basin in Xinjiang that produces indeterminate labyrinthodonts and ?*Lystrosaurus* are of Lootsbergian age.

Southwest of the Transantarctic Mountains in southern Antarctica, the lower part of the Fremouw Formation produces a vertebrate fossil assemblage of Lootsbergian age that includes: the temnospondyls *Austrobrachyops jenseni* Colbert and Cosgriff, *Cryobatrachus kitchingi* Colbert and Cosgriff, and a rhytidosteid; the procolophonid *Procolophon trigoniceps* Owen; the eosuchian *Prolacerta broomi* Parrington; the prolacertilian *Ericiolacerta parva* Watson; a proterosuchid or erythrosuchid, and a rauisuchian; the dicynodonts *Myosaurus gracilis* (Haughton), *Lystrosaurus murrayi* (Huxley), *L. curvatus* (Owen), *L. maccaigi* (Seeley); the cynodont *Thrinaxodon liorhinus* Seeley; and the scaloposaurs *Padaeosaurus parvus* Colbert and Kitching, and *Rhigosaurus glacialis* Colbert and Kitching. This has been referred to as the lower Fremouw fauna or lower tetrapod fauna of the Fremouw Formation (Colbert, 1972, 1991).

In India, the Panchet Formation along the Damodar River northwest of Calcutta has produced a Lootsbergian vertebrate assemblage that includes the lydekkerinid *Lydekkerina panchetensis* Tripathi, the ?benthosuchid *Indobenthosuchus* *panchetensis* Tripathi, the ?capitosaurids *Pachygonia incurvata* Huxley and *Labyrinthodon panchetensis* Tripathi, the indobrachyopid *Indobrachyops panchetensis* Huene and Sahni, the trematosaurids *Gonioglyptus longirostris* Huxley, *Indolyrocephalus huxleyi* (Lydekker) and *I. panchetensis* Tripathi, a procolophonid, the proterosuchian *Proterosuchus* sp. and four nominal species of *Lystrosaurus* (*L. murrayi*, *L. platyceps*, *L. macccaigi* and *L. rajurkari*) (Huxley, 1865; Lydekker, 1882; Sahni and von Huene, 1958; Tripathi, 1961, 1969; Tripathi and Satsangi, 1963; Hughes, 1963).

In the Russian Urals, the Lootsbergian interval is equivalent to Zone V of Efremov (1937, 1952), which is now called the Vokhmian horizon of the Vetlugan Series (Superhorizon). Tetrapod taxa include: the temnospondyls *Luzocephalus blomi* Shishkin, *Benthosuchus uralensis* (Ochev), *B. sushkini* Efremov, *B. bashkirikus* Ochev; *Wetlugasaurus angustifrons* Riabinin, *W. kzilsajensis* Ochev, *W. calaevi* (Kuzmin), *W. cornutus* Efremov, *W. volgensis* (Hartman-Weinberg and Kuzmin), *W. lehmani* Ochev, *Tupilakosaurus wetlugensis* Shishkin, and *Plagiorophus paraboliceps* Konzhukova; the prolacertid *Microcnemus* sp.; the proterosuchids *Chasmatosuchus* sp. and *Exilisuchus tuberculatus* Ochev; and the dicynodont *Lystrosaurus georgi* Kalandadze (Shishkin et al., 1995b).

The Wordy Creek Formation in eastern Greenland produces the temnospondyls *Luzocephalus kochi* (Säve-Söderbergh), *L. johanssoni* (Säve-Söderbergh), *L. rapax* (Säve-Söderbergh), *Wetlugasaurus groenlandicus* Säve-Söderbergh, *Stoschiosaurus nielseni* Säve-Söderbergh and *Tupilakosaurus heilmani* Nielsen (Säve-Söderbergh, 1935; Nielsen, 1954). The stratigraphically lowest record of *Luzocephalus* here is in the *Ophiceras commune* Ammonite Zone, and the genus extends up through the '*Proptychites rosenkrantzi* Zone'. Most of the Wordy Creek Formation amphibians come from the younger '*Anodontophora fassarensis* beds', which are the youngest Lower Triassic strata in this section (Nielsen, 1935; Säve-Söderbergh, 1935). This indicates a range of *Luzocephalus* from late Griesbachian through early Dienerian (middle Induan), but the other temnospondyl taxa are of middle or late Dienerian (late Induan) age (Trümpy, 1961; Silberling and Tozer, 1968; Tozer, 1994).

4.5. Marine cross-correlation

Direct cross-correlation of the Lootsbergian to part of the Induan is provided by the occurrence of characteristic Lootsbergian temnospondyls in ammonite-bearing Induan strata of the Wordy Creek Formation in eastern Greenland (Trümpy, 1961). Apparently, the beginning of the Lootsbergian does not correspond to the beginning of the Triassic. The FAD of *Lystrosaurus* has long been assumed to equate to the beginning of the Triassic, but a close correlation has not been documented. Whether or not the end of the Lootsbergian correlates to the end of the Induan also is uncertain. Ochev and Shishkin (1989) and Shishkin and Ochev (1992) equated the Lootsbergian with the entire Early Triassic ('Scythian'), but marine cross-correlation of the Nonesian suggests this is incorrect (see below).

The stratigraphic ranges of *Lystrosaurus* and *Dicynodon* have long been known to overlap in northwestern China (Cheng, 1993; Cheng and Lucas, 1993; Lucas, 1993a) and in the Karoo basin of South Africa (Keyser, 1973a; Lucas et al., 1994b; Smith, 1995). King and Jenkins (1997) recently described a single skull of *Lystrosaurus* from the Madumabisa Mudstones of the Luangwa Valley, Zambia, associated with the 'characteristic Permian' genera *Oudenodon*, *Dicynodon*, *Diictodon* and *Procynosuchus*. The Chinese, South African and Zambian records thus suggest that the FAD of *Lystrosaurus* is of Late Permian age. Therefore, King and Jenkins (1997) (p. 153) stated that "isolated specimens of the genus should no longer be used for biostratigraphical purposes", meaning that they cannot be used to distinguish Triassic from Permian strata. I endorse that narrow conclusion, but stress that all records of *Lystrosaurus* are of great biochronological significance because they identify Lootsbergian time.

4.6. Comments

Most Lootsbergian vertebrate fossil assemblages are readily recognized by the presence of *Lystrosaurus*. However, temnospondyl-dominated assemblages that lack *Lystrosaurus* are more difficult to correlate. I have used the temporal overlap of *Lystrosaurus* and the amphibians *Tupilakosaurus* and *Luzocephalus* in Russian strata as the primary basis for correlation of dicynodont-dominated to temnospondyl-dominated assemblages.

Cosgriff (1984) assigned several temnospondyl-dominated assemblages to his A1 'horizon' (= Lootsbergian) that lack any index taxa of the Lootsbergian–Knocklofty Sandstone/Shale in SE Tasmania (Cosgriff, 1974), the Sticky Keep Formation in Svalbard (Wiman, 1910, 1915; Nilsson, 1942, 1943; Cox and Smith, 1973), the upper Andavakoera Formation (middle Sakamena Group) in NW Malagasy (Lehman, 1961, 1966), and the Arcadia Formation of southern Queensland (Warren, 1991). However, most of these assemblages are clearly younger than Lootsbergian and are assigned a Nonesian age (see below).

5. Nonesian LVF

5.1. Definition

I propose the term Nonesian LVF to refer to the time equivalent to the *Cynognathus* Assemblage Zone from the upper two-thirds of the Burgersdorp Formation in the Karoo basin of South Africa (Kitching, 1995). The assemblage zone spans a section as much as 600 m thick (Fig. 3). The type section of the *Cynognathus* Assemblage Zone encompasses Nonesi's Nek, from which the name Nonesian is derived (Kitching, 1995). Nonesian time begins with the FAD of *Cynognathus*. The end of the Nonesian is the beginning of the Perovkan LVF, which is defined by the FAD of *Shansiodon*.

Broom (1906, 1907) coined the name *Cynognathus* 'beds', which was later transmuted to 'zone' by other workers (Watson, 1914a,b; Kitching, 1970, 1977). Keyser and Smith (1978) renamed it the *Kannemeyeria* Assemblage Zone, and Keyser (1979) termed it the *Kannemeyeria–Diademodon* Assemblage Zone. Kitching (1984) called it the *Cynognathus–Diademodon* Assemblage Zone. The term *Cynognathus* Assemblage Zone has been used most recently (Kitching, 1995).

5.2. Index fossils

The following tetrapod genera are restricted to Nonesian time and are widespread and/or common enough to be considered index fossils: *Parotosuchus*, *Trematosuchus*, *Erythrosuchus*, *Cynognathus*, *Diademodon*, *Trirachodon*, *Kannemeyeria cristarhynchus* (Fig. 5).

5.3. Type assemblage

The type assemblage of the Nonesian LVF is the *Cynognathus* Assemblage Zone of the Karoo basin. The following tetrapod taxa are present: the temnospondyls *Batrachosuchus watsoni* Haughton, *B. browni* Broom, *Laidleria gracilis* Kitching, *Parotosuchus dirus* Chernin, *P. albertyni* (Broom), *P. africanus* (Broom), *P. haughtoni* (Broili and Schröder), *Trematosuchus kannemeyeri* (Broom) and *T. sobeyi* (Haughton); the captorhinids *Microthelodon parvus* (Broom), *Myocephalus crassidens* Broom, *Thelegnathus browni* Broom, *T. oppressus* Broom and *T. spinigenus* Broom; the ?sphenodontid (or ?procolophonid) *Palacrodon browni* Broom; the rhynchosaurs *Howesia browni* Broom and *Mesosuchus browni* Broom; the archosaurs *Erythrosuchus africanus* Broom and *Euparkeria capensis* Broom; the dicynodonts *Kannemeyeria simocephalus* (Weithofer) and *Kombuisuia frerensis* Hotton; the therocephalians *Bauria cynops* Broom, *Melinodon simus* Broom, *Sesamodon browni* (Broom) and *Watsoniella breviceps* Broili and Schröder; the cynodonts *Bolotridon frerensis* (Seeley), *Cynognathus crateronotus* Seeley, *Diademodon tetragonus* Seeley, *Trirachodon berryi* Seeley and *T. kannemeyeri* Seeley.

Kitching (1977) reviewed the *Cynognathus* Assemblage Zone localities, and Kitching (1995) provided a recent synopsis of the stratigraphic ranges of the genera (Fig. 3). Watson (1942) and Kitching (1977) subdivided the *Cynognathus* Assemblage Zone into two subzones (Fig. 6). Hancox and Rubidge (1994), Hancox et al. (1995) and Shishkin et al. (1995a) divided the *Cynognathus* Assemblage Zone into three successive zones: (1) *Kestrosaurus* acme zone; (2) '*Parotosuchus*' *africanus* acme zone; and (3) advanced capitosauroid zone. Kitching (1995), however, made no attempt at subdivision, and no formal subdivisions are advocated here.

5.4. Principal correlatives

Principal correlatives of the type *Cynognathus* Assemblage Zone are: upper Fremouw Formation,

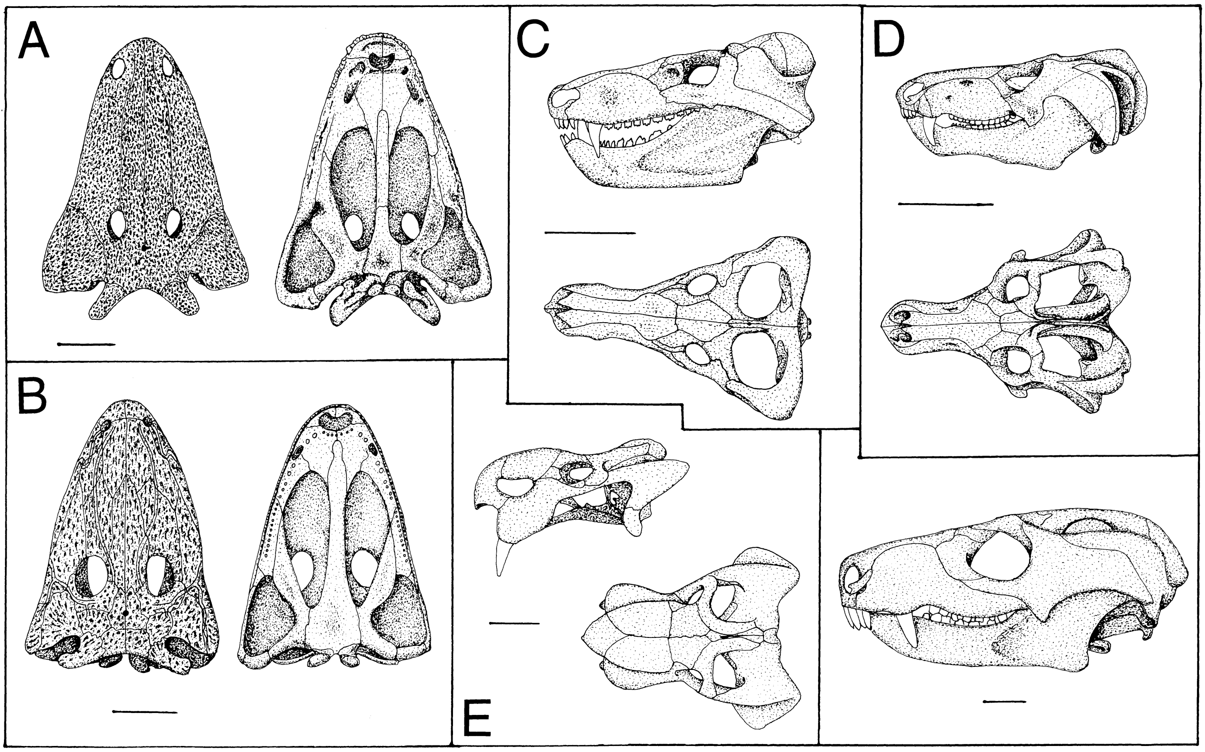


Fig. 5. Some Nonesian index fossils. (A) *Parotosuchus*, dorsal (left) and ventral (right) views of skull. (B) *Eryosuchus*, dorsal (left) and ventral (right) views of skull. (C) *Cynognathus*, lateral (above) and dorsal (below) views of skull. (D) *Diademodon*, lateral (above) and dorsal (below) views of skull. (E) *Kannemeyeria cristarhynchus*, lateral (above) and dorsal (below) views of skull. (F) *Trirachodon*, lateral view of skull. (A, B) After Shishkin; (C–E) after Kitching; (F) after Hopson. Bar scales: (A–E) 10 cm long; (F) 10 mm long.

Antarctica; Petropavlovsk Formation ('Yarenskiy horizon') in the Russian Urals; Wupatki and Torrey formations of the Moenkopi Group, Arizona–Utah, USA; Puesto Viejo and Rio Mendoza formations, Argentina; lower part of Ermaying Formation, Ordos basin, China; Omingonde Formation, Namibia; lower N'tawere Formation, Zambia; K7 horizon of the Kingori Sandstone, Tanzania; and Sticky Keep Formation of Svalbard.

In Antarctica, the upper part of the Fremouw Formation produces capitosaurid temnospondyls, *Cynognathus* sp., a diademodontid and a kannemeyeriid (Colbert, 1991; Hammer, 1995; W.R. Hammer, written commun., 1998).

The Petropavlovsk Formation ('svita') in the Russian Urals (so-called 'Yarenskiy horizon') produces: the temnospondyls *Parotosuchus orenbergensis* (Konzhukova), *P. orientalis* Ochev, *Yarengia* sp., *Batrachosuchoides* sp., *Melanopelta antiqua* Shishkin and *Rhytidosteus uralensis* Shishin and Novikov; the procolophonids *Burtensia burtensis* (Ochev) and *Kapes majmesculae* (Ochev); a prolacertid; the erythrosuchid *Garjainia prima* Ochev; and the rauisuchid *Jaikosuchus magnus* (Ochev) (Shishkin et al., 1995b).

The Torrey Formation of the Moenkopi Group in Utah, USA yielded a skull of *Parotosuchus* sp. (I. Novikov, pers. commun., 1993), and specimens of *Parotosuchus peabodyi* (Welles and Cosgriff) are from the Wupatki Formation. The Torrey Formation overlies the early Olenikian (Smithian) ammonite-bearing Sinbad Formation (Blakey, 1974), whereas the Wupatki is clearly younger than the late Olenikian Virgin Limestone (e.g., McKee, 1954; Morales, 1987; Steiner et al., 1993).

In Argentina, the upper part of the Puesto Viejo Formation produces the dicynodont *Kannemeyeria argentinensis* Bonaparte, the traversodontid *Pas-*

ZONE	WATSON (1942) KITCHING (1977)		HANCOX et al. (1995), SHISKIN et al. (1995)	
Cynognathus Assemblage Zone	upper	no *Kannemeyeria*, *Erythrosuchus* rare	upper	advanced capitosauroid zone
	lower	*Kannemeyeria* and *Erythrosuchus* common	middle	"*Parotosuchus*" *africanus* acme zone
			lower	*Kestrosaurus* acme zone

Fig. 6. Proposed subdivisions of the *Cynognathus* Assemblage Zone.

cualagnathus polanskii Bonaparte, and the cynognathid *Cynognathus minor* Bonaparte (Bonaparte, 1970, 1978, 1982). The co-occurrence of *Cynognathus* and *Kannemeyeria* justifies a Nonesian age assignment. The correlative fauna from the middle part of the Rio Mendoza Formation includes *Kannemeyeria* (*Vinceria andina* Bonaparte is not *Shansiodon*, as Lucas (1993e) suggested, but instead is *Kannemeyeria*), the traversodontids *Andescynodon mendozensis* Bonaparte and *Rusconiodon mignonei* Bonaparte, and the galeosaurid *Cromptodon mamiferoides* Bonaparte.

Bonaparte (1981) described dicynodonts and proterosuchian postcrania from the lower part of the Puesto Viejo Formation that he referred to as the Agua de los Burros local fauna. He assigned the dicynodonts to '*Vinceria*' (= *Kannemeyeria*) and claimed correlation to the *Lystrosaurus* Assemblage Zone based on a mean value of K/Ar ages of 232 ± 4 Ma from basalts and tuffs that bracket the fossils (Valencio et al., 1975: fig. 2). Given that the Permo–Triassic boundary is approximately 250 Ma (Renne et al., 1995), the Argentinian dates do not support Bonaparte's correlation, nor do the fossils, which suggest a Nonesian age.

In China, the lower Ermaying Formation in the Ordos basin produces a vertebrate fauna upon which Lucas (1993a) based the Ordosian LVF. Taxa present are the procolophonid *Pateodon huanghoensis* Chow and Sun, the proterosuchian *Guchengosuchus shiguainensis* Peng, the euparkeriids *Turfanosuchus shagenduensis* Wu and *Halazhaisuchus qiaoensis* Wu, the ordosiid therocephalians *Ordosiodon linchenyuenensis* Young and *O. youngi* Hou, the therocephalian *Yikezhaogia megafenestrala* Li, and the dicynodonts *Parakannemeyeria xingxianensis* Cheng, *Kannemeyeria* (= *Shaanbeikannemeyeria*) *sanchuanheensis* Cheng and *K. buerdongia* Li.

The Omingonde Formation in Namibia produced an eryopoid temnospondyl, the dicynodonts *Kannemeyeria simocephalus* Weithofer, *Dolichuranus primaevus* Keyser and *Rhopalorhinus etionensis* Keyser, the bauriamorph *Herpetogale marsupialis* Keyser, and the cynodonts ?*Cynognathus* sp., *Diademodon tetragonus* Seeley, *Titanogomphodon crassus* Keyser and *Trirachodon* sp. (Keyser, 1973b,c, 1978; Pickford, 1995). The lower part of the N'tawere Formation in Zambia produces *Diademodon* and *Kannemeyeria* (Crozier, 1970). In the Ruhuhu Valley of Tanzania, the K7 horizon of the Kingori Sandstone Formation of Stockley (1932) yields *Kannemeyeria* (Cruickshank, 1986).

Temnospondyls of the Sticky Keep Formation in Svalbard co-occur with early Olenikian (Smithian) ammonites (Buchanan et al., 1965; Tozer, 1967). The temnospondyls are *Sasenisaurus spitsbergensis* (Wiman), *Peltostega erici* Wiman, *P. wimani* Nilsson, *Aphanerama* (= *Lonchorhynchus*) *rostratum* Woodward, *Lyrocephaliscus euri* (Wiman), *Teretrema acuta* Wiman, and *Boreaosaurus thorslundi* Nilsson (Wiman, 1910, 1915; Nilsson, 1942, 1943; Cox and Smith, 1973).

The Yerrapalli Formation in India produces a Nonesian-age assemblage that includes the temnospondyl *Parotosuchus rajareddyi* (Roychowdhury), a brachyopid, a trirachodontid, a proterosuchian, a pseudosuchian and the dicynodonts *Wadiasaurus indicus* Roychowdhury and *Kannemeyeria* (= *Rechnisaurus*) *cristarhynchus* (Roychowdhury) (Roychowdhury, 1970a,b).

5.5. Marine cross-correlation

The occurrence of *Parotosuchus* in marine Olenikian strata of the Mangyshlak Peninsula in western Kazakstan (Lozovsky and Shishkin, 1974) is the most direct cross-correlation of the Nonesian to the SGCS. *Aphanerama* and *Parotosuchus* records in Svalbard and North America also support correlation of the Nonesian with at least part of the Olenikian.

Ochev and Shishkin (1989) and Shishkin et al. (1995a) suggested that the later part of the Nonesian is of Middle Triassic (Anisian) age. They based this argument on the perceived stage of evolution of temnospondyls from the upper part of the *Cynognathus* Assemblage Zone in South Africa. In so doing, they relied heavily on a perceived linear evolutionary trajectory in the closure of the otic notch that culminates, for example, in taxa such as the Middle Triassic capitosaur *Eocyclotosaurus* that have completely enclosed notches. However, the linear nature of this trajectory is doubtful, as Schoch (1997) has demonstrated by showing that closure of the otic notch does not necessarily correlate with other morphological changes. Therefore, correlations based on perceived evolutionary grade in temnospondyls, such as those advocated by Shishkin and his co-authors, are doubtful.

5.6. Comments

In the Karoo basin of South Africa, there is a virtually complete turnover in the tetrapod fauna at the beginning of the Nonesian. The lithostratigraphy does not suggest a substantial unconformity here, so this appears to be a real (at least local) extinction of the Lootsbergian fauna.

Most Nonesian vertebrate assemblages are readily recognized by the presence of *Cynognathus* and/or *Diademodon*. *Parotosuchus* is a key temnospondyl taxon to correlate the therapsid-dominated assemblages to the temnospondyl-dominated assemblages. However, note that the genus is in serious need of taxonomic revision (i.e., *Parotosuchus* is a 'wastebasket' taxon for most capitosaurs with open otic notches), so its biochronological significance may not be stable (Damiani, 1997).

Nonesian time may be relatively long, and subdivision has been attempted. However, the data supporting this subdivision remain to be published, so no formal subdivision of the Nonesian is advocated here.

6. Perovkan LVF

6.1. Definition

I propose the term Perovkan LVF to refer to the time equivalent to the vertebrate fossil assemblage of the Donguz 'svita' (= Formation) in the Russian Urals (Shishkin et al., 1995b). I term this the *Shansiodon* Assemblage Zone, after the distinctive dicynodont *Shansiodon* (= *Rhinodicynodon*). These fossils are from sites in an approximately 175-m-thick section (Fig. 7) exposed in the Donguz River drainage near the city of Perovka, from which the name of the LVF is taken. The beginning of the Perovkan is defined by the FAD of the dicynodont *Shansiodon*. The end of the Perovkan is the beginning of the Berdyankian, which is defined by the FAD of the temnospondyl *Mastodonsaurus*.

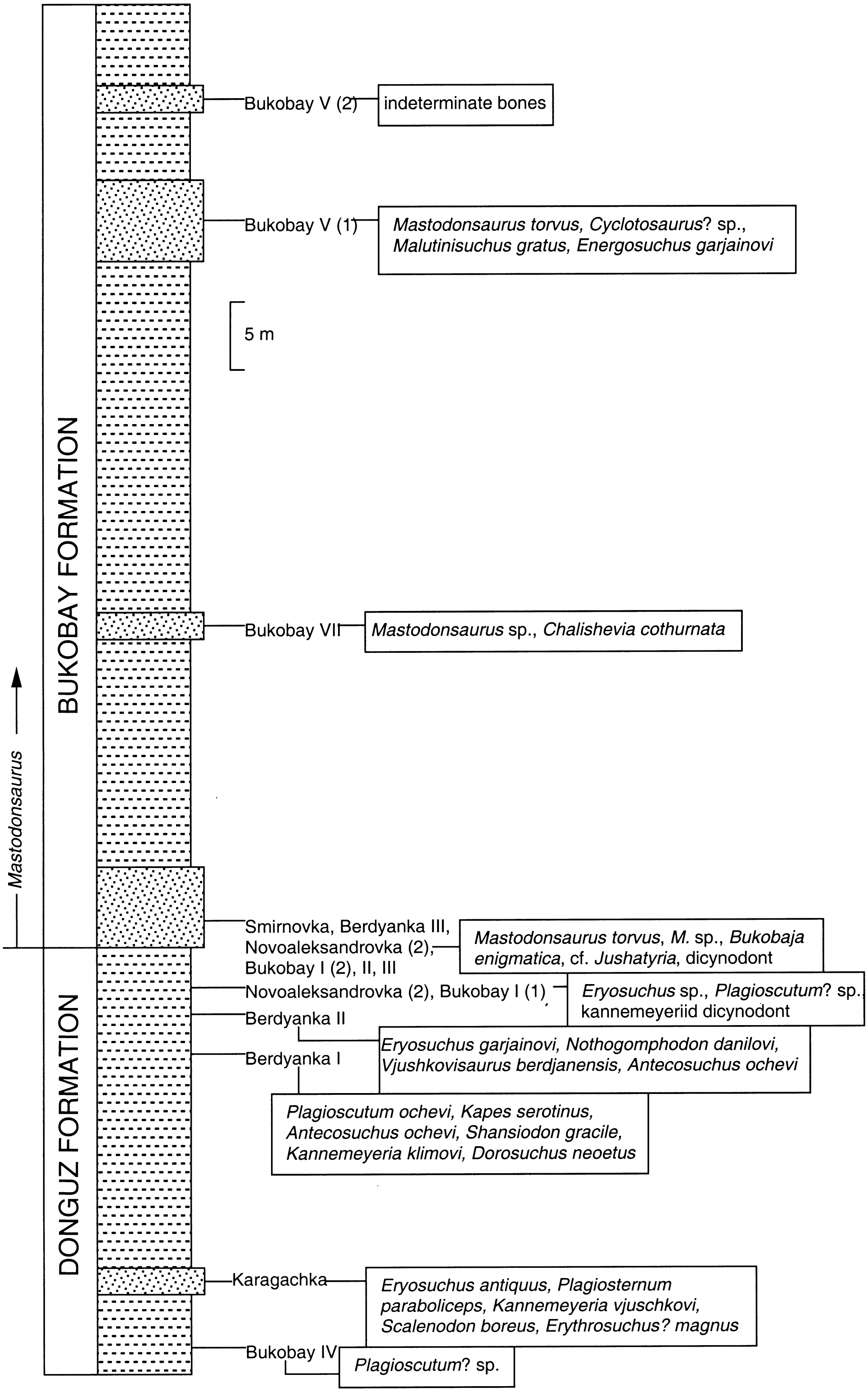
6.2. Index fossils

The following tetrapod genera are common and/or widespread enough to be useful index taxa of the Perovkan: *Eryosuchus*, *Eocyclotosaurus*, *Shansiodon*, *Scalenodon*, *Parakannemeyeria*, *Sinokannemeyeria*, *Kannemeyeria simocephalus* (Fig. 8).

6.3. Type assemblage

Three principal sites in the Donguz Formation produce the following taxa: the temnospondyls *Eryosuchus tverdochlebovi* Ochev, *E. garjainovi* Ochev, *E. antiquus* Ochev, *Bukobaja*? sp., *Plagiosternum paraboliceps* (Konzhukova), and *Plagioscutum ochevi* Shishkin; the procolophonid *Kapes serotinus* Novikov; a prolacertid; the proterosuchid *Sarmatosuchus ochevi* Sennikov; the erythrosuchid *Erythrosuchus magnus* Ochev; the rauisuchids *Vjushkovisaurus berdjanensis* Ochev, *Dongusuchus efremovi* Sennikov, and *Dongusia colorata* Huene; the euparkeriid *Dorosuchus neoetus* Sennikov; the dicynodonts *Kannemeyeria* spp. (I consider *Rhadiodromus*, *Rabidosaurus*, *Edaxosaurus*, *Calleonassus* and *Rhinocerocephalus* to be

Fig. 7. Stratigraphic distribution of tetrapods in the Donguz and Bukobay formations of the Russian Urals (based on data in Shishkin et al., 1995b).


Bukobay V (2)
indeterminate bones
Bukobay V (1)
Mastodonsaurus torvus, *Cyclotosaurus*? sp., *Malutinisuchus gratus*, *Energosuchus garjainovi*
5 m
BUKOBAY FORMATION
Bukobay VII
Mastodonsaurus sp., *Chalishevia cothurnata*
Mastodonsaurus
Smirnovka, Berdyanka III, Novoaleksandrovka (2), Bukobay I (2), II, III
Mastodonsaurus torvus, *M.* sp., *Bukobaja enigmatica*, cf. *Jushatyria*, dicynodont
Novoaleksandrovka (2), Bukobay I (1)
Eryosuchus sp., *Plagioscutum*? sp., kannemeyeriid dicynodont
Berdyanka II
Eryosuchus garjainovi, *Nothogomphodon danilovi*, *Vjushkovisaurus berdjanensis*, *Antecosuchus ochevi*
Berdyanka I
Plagioscutum ochevi, *Kapes serotinus*, *Antecosuchus ochevi*, *Shansiodon gracile*, *Kannemeyeria klimovi*, *Dorosuchus neoetus*
DONGUZ FORMATION
Karagachka
Eryosuchus antiquus, *Plagiosternum paraboliceps*, *Kannemeyeria vjuschkovi*, *Scalenodon boreus*, *Erythrosuchus*? *magnus*
Bukobay IV
Plagioscutum? sp.

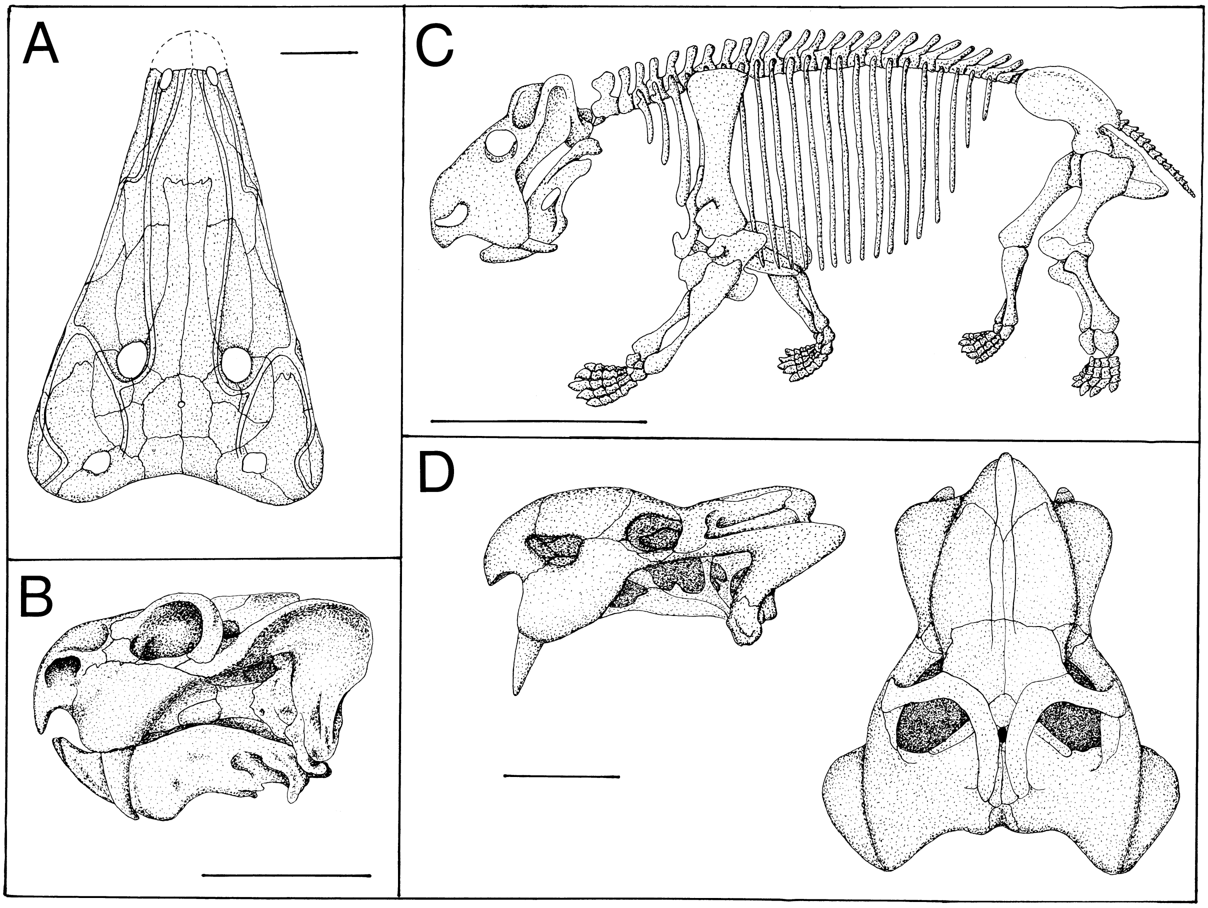


Fig. 8. Some Perovkan index fossils. (A) *Eocyclotosaurus*, dorsal view of skull. (B) *Shansiodon*, lateral view of skull and lower jaw. (C) *Sinokannemeyeria*, lateral view of skeleton. (D) *Kannemeyeria simocephalus*, lateral (left) and dorsal (right) views of skull. (A) After Ortlam; (B) after Kalandadze; (C) after Sun; (D) after Bandyopadyhay. Bar scales: (A) 5 cm long; (B, D) 10 cm long; (C) 0.5 m long.

junior synonyms of *Kannemeyeria*) and *Shansiodon* (= *Rhinodicynodon*) *gracile* (Kalandadze); the therocephalians *Dongusaurus schepetovi* Vyushkov and *Nothogomphodon danilovi* Tatarinov; the diademodontid *Scalenodon boreus* Tatarinov; and the traversodontid *Antecosuchus ochevi* Tatarinov (Shishkin et al., 1995b).

6.4. Principal correlatives

Principal correlatives of the type Perovkan assemblage are from the upper Ermaying Formation, Ordos basin, China; lower Kelamayi Formation, Junggur basin, Xinjiang, China; Holbrook and Anton Chico members of the Moenkopi Formation, western USA; middle–upper Buntsandstein, Germany; lower Zarzaitine Formation, Algeria; lower Manda Formation, Tanzania; and the Otter Sandstone of the United Kingdom.

The upper part of the Ermaying Formation in the Ordos basin produces what has been called the ‘*Sinokannemeyeria* fauna’ or ‘kannemeyeriid fauna’ of China (e.g., Sun, 1972; Cheng, 1981). Lucas (1993a) based the Ordosian LVF on this assemblage. The vertebrate fossil assemblage includes indeterminate labyrinthodonts, the procolophonid *Neoprocolophon asiaticus* Young, the erythrosuchids *Shansisuchus shansisuchus* Young and *S. kuyeheensis* Cheng, the ?ornithosuchid *Fenhosuchus cristatus* Young, the ?euparkeriid *Wangisuchus tzeyii* Young, the cynodont *Sinognathus gracilis* Young, and the dicynodonts *Shansiodon wangi* Ye, *S. wuhsiangensis* Ye, *S. wupuensis* Cheng, *Sinnokannemeyeria pearsoni* Young, *S. sanchuanheensis* Cheng, *Parakannemeyeria dolicocephala* Sun, *P. youngi* Sun, *P. ningwuensis* Sun and *P. shenmuensis* Cheng.

In the Junggur basin of Xinjiang, the lower part of the Kelamayi (= Karamay) Formation produces a correlative vertebrate fauna that consists of indeterminate labyrinthodonts (including the holotype of the *nomen dubium* '*Parotosaurus*' [= *Parotosuchus*] *turfanensis* Young: Lucas and Hunt, 1993c), the euparkeriid *Turfanosuchus dabanensis* Young, the erythrosuchid *Garjainia* (= *Youngosuchus* Sennikov in Kalandadze and Sennikov, 1985: Parrish, 1992) *sinensis* Young, and the dicynodont *Parakannemeyeria brevirostris* Sun. The bauriid therapsid *Traversodontoides wangwuensis* Young from Jiyuan, Henan may be of Perovkan age (Cheng, 1981; Sun, 1989).

The Holbrook and Anton Chico members of the Moenkopi Formation in Arizona–New Mexico, USA, yield the characteristic Perovkan capitosauroid *Eocyclotosaurus*, close to *E. lehmanni* from the upper Buntsandstein (Lucas and Morales, 1985; Lucas and Hunt, 1987; Morales, 1987). A *Shansisuchus*-like erythrosuchid recently discovered in the Anton Chico Member (Lucas et al., 1998b) further supports a Perovkan age assignment.

In Germany, the upper Buntsandstein (Röt) has produced *Eocyclotosaurus lehmani* and *E. woschmidti* (Heyler, 1969, 1976; Ortlam, 1970; Kamphausen and Morales, 1981). Other middle–upper Buntsandstein tetrapods include the temnospondyl *Trematosaurus brauni* Burmeister, procolophonids (e.g., *Koiloskiosaurus*), and *Tanystropheus antiquus* Huene (Kuhn, 1971), and are of probable Perovkan age.

The lower Zarzaitine Formation, Algeria, produces the temnospondyls *Wellesaurus bussoni* (Lehman), '*Parotosaurus*' *lapparenti* Lehman, a brachyopid and an indeterminate diapsid reptile (Lehman, 1957, 1971; Jalil, 1990, 1993, 1994).

The lower Manda Formation in Tanzania produces the dicynodont *Angonisaurus cruickshanki* Cox and Li, the diademodontid *Scalenodon* sp., the rhynchosaur *Stenaulorhynchus*, the pseudosuchian '*Mandasuchus*' and the dicynodont *Shansiodon* (= *Tetragonius*) *njalilus* (Huene) (von Huene, 1938a,b; Crompton, 1955; Cruickshank, 1965, 1967; Cox and Li, 1983).

The Otter Sandstone in Devon, United Kingdom, yields the temnospondyl *Eocyclotosaurus* sp., the rhynchosaur *Rhynchosaurus spenceri* Benton, *Tanystropheus* sp., a procolophonid, a rauisuchian and a ?ctenosauriscid archosaur (Benton et al., 1994). As Milner et al. (1990) stressed, '*Mastodonsaurus*' *lavisi* Seeley from the Otter Sandstone is a *nomen dubium* upon which it is risky to draw stratigraphic conclusions.

6.5. Marine cross-correlation

No direct vertebrate-based correlation can be made of the Perovkan to the SGCS. I follow Anderson and Cruickshank (1978), who advocated cross-correlation to the early Anisian. This is justified by two observations: (1) marine facies of the lower Röt contain early Anisian conodonts (e.g., Kozur, 1993), which justifies assigning *Eocyclotosaurus* records in Germany an early Anisian age; and (2) some Perovkan tetrapod assemblages overlie Nonesian assemblages that can be reliably cross-correlated to at least part of the Olenikian (see above). The possibility that part of the Perovkan correlates to the late Olenikian needs further evaluation. It seems very unlikely, though, that any Perovkan vertebrate assemblage is of Ladinian age.

6.6. Comments

Perovkan tetrapod assemblages are best known in Russia and China where they contain numerous dicynodonts. Correlatives are either dicynodont dominated (Manda, Omingonde) or amphibian dominated (Moenkopi, upper Buntsandstein).

It seems likely that no Perovkan vertebrate assemblage is younger than early Anisian. Although Perovkan time is the interval up to the beginning of the Berdyankian, the latter part of the time interval may lack vertebrate representation. This suggests that there is a need here for another LVF between the Berdyankian and Perovkan, though I cannot define and characterize one at present because of inadequate data.

7. Berdyankian LVF

7.1. Definition

I propose the term Berdyankian LVF for the time equivalent to the vertebrate fossil assemblage of the Bukobay Formation (‘svita’) in the Russian Urals. Relevant vertebrate-fossil localities are near the Berdyank River, from which the LVF takes its name. The type Berdyankian vertebrate assemblage is directly superposed on the type Perovkan assemblage (Fig. 7). The beginning of the Berdyankian is defined by the FAD of *Mastodonsaurus*, whereas the end is the beginning of the Otischalkian, which is defined by the FAD of *Paleorhinus*.

7.2. Type assemblage

The assemblage from the Bukobay Formation includes the following taxa: the temnospondyls *Mastodonsaurus torvus* Konzhukova, *Bukobaja enigmatica* Ochev, *Cyclotosaurus*? sp. and *Plagioscutum caspiense* Shishkin, *Plagiosternum danilovi* Shishkin; the erythrosuchid *Chalishevia cothurnata* Ochev; the rauisuchid *Jushatyria vjushkovi* Sennikov; the dicynodonts ‘*Elephantosaurus jachimovitschi*’ Vyushkov and a kannemeyeriid (‘*Elatosaurus facetus*’ Kalandadze *nomen dubium*) (Shishkin et al., 1995b).

7.3. Index fossils

The following tetrapod genera are common and/or widespread enough to be index fossils of the Berdyankian: *Dinodontosaurus*, *Mastodonsaurus*, *Exaeretodon*, *Massetognathus*, *Stahleckeria* (Fig. 9).

7.4. Principal correlatives

The Lettenkohle in Germany and the Chanarian LVF localities in Argentina and Brazil are the principal correlatives of the Berdyankian type assemblage.

The Lettenkohle record is important because it establishes the Ladinian age of the Berdyankian. The Lettenkohle fossils are from the Grenze bonebed, the laterally equivalent/overlying Vitriolschiefer and the Kupferzell locality, so they are above the unconformity that separates the Keuper from the underlying Muschelkalk. Lettenkohle tetrapods include: the temnospondyls *Mastodonsaurus jaegeri* (Owen), *Plagiosternum* spp. and *Kupferzella wildi* Schoch; a *Ticinosuchus*-like rauisuchid; the prolacertilian *Tanystropheus*; and small cynodonts (Wild, 1978, 1980; Schoch, 1997). Palynology suggests that the Lettenkohle is early Ladinian (lowermost Longoboardian: Visscher et al., 1993), or early/middle Ladinian (upper Fassan: Hagdorn and Gluchowski, 1993). A *Dinodontosaurus*-like humerus from the Vitriolschiefer (Lucas and Wild, 1995) may link the Lettenkohle to the South American Chanarian.

The Chañares local fauna from the Ischichuca (formerly Chañares) Formation of the Ischigualasto–Villa Unión basin of NW Argentina produces: the ‘thecodonts’ *Luperosuchus fractus* Romer, *Lagerpeton chanarensis* Romer, *Lagosuchus talampayensis* Romer, *L. lilloensis* Bonaparte, *Chanaresuchus bonapartei* Romer, *Gualosuchus reigi* Romer, *Gracilisuchus stipanicicorum* Romer, and *Lewisuchus admixtus* Romer; the dicynodont *Dinodontosaurus turpior* (Huene); the traversodontids *Massetognathus pascuali* Romer, *M. teruggii* Romer, *M. major* Romer and *Megagomphodon oligodens* Romer; the chiniquodontids *Probelesodon lewisi* Romer, and *P. minor* Romer; and the probainognathid *Probainognathus jenseni* (Bonaparte, 1970; Romer, 1973; Lucas and Harris, 1996). Bonaparte (1966, 1967, 1982) based the Chanarian ‘provincial age’ on this assemblage.

The lower part of the Santa Maria Formation in the Paraná basin of Rio Grande do Sul produces vertebrate fossil assemblages from Candelaria and Chiniquá considered by Barberena (1977) and Barberena et al. (1985) to be two different local faunas of different ages. I regard them as a single biostratigraphic assemblage that includes: the procolophonid *Candelaria barbourii* Price; the thecodonts *Prestosuchus loricatus* Huene, *Prestosuchus chiniquensis* Huene, *Procerosuchus celer* Huene, and *Spondylosoma absconditum* Huene; the dicynodonts *Dinodontosaurus turpior* (Huene) and *Stahleckeria potens* (Huene) (= *Barysoma lenzii* [Romer and Jensen]); the chiniquodontids *Chiniquodon theotonicus* Huene and *Chiniquodon* sp.; and the traversodontids *Massetognathus ochagaviae* Barberena and Daemon, *Belesodon magnificus* Huene, *Belesodon* sp., *Traver-*

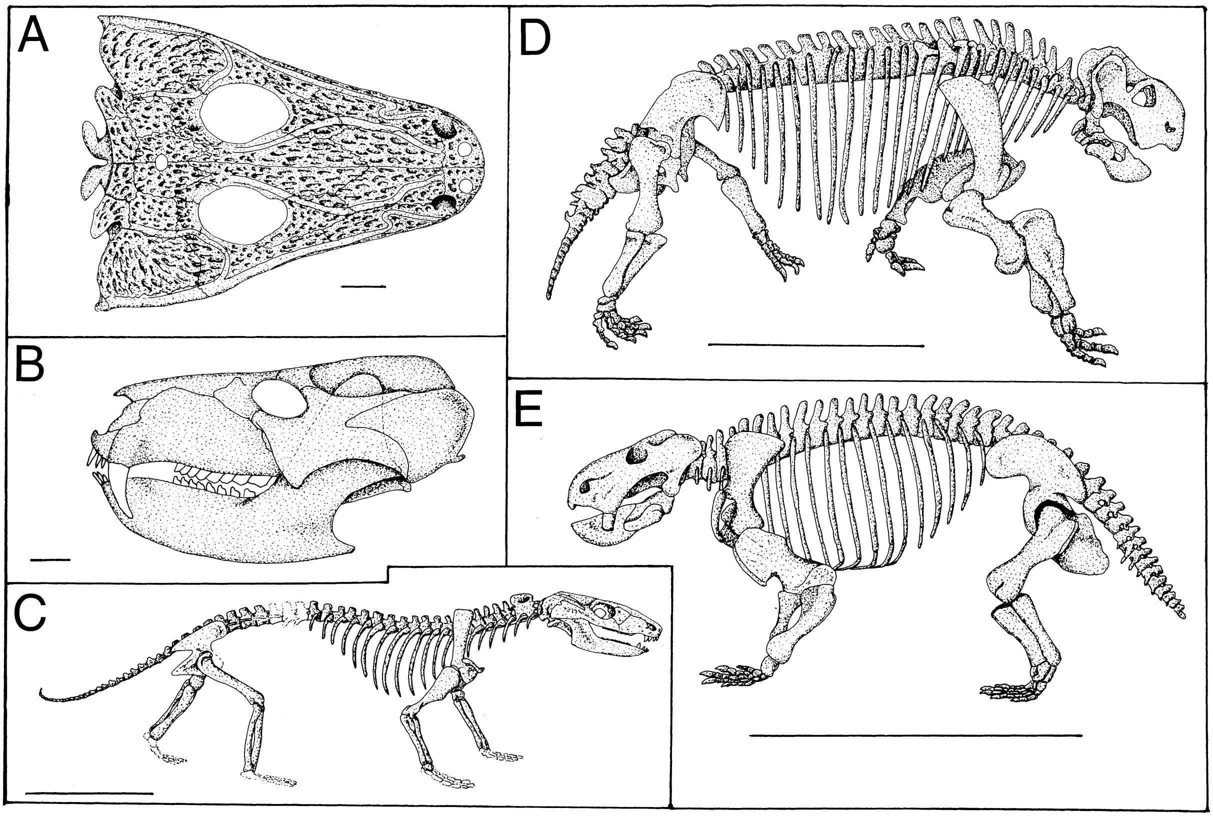


Fig. 9. Some Berdyankian index fossils. (A) *Mastodonsaurus,* dorsal view of skull. (B) *Exaeretodon,* lateral view of skull and lower jaw. (C) *Massetognathus,* lateral view of skeleton. (D) *Stahleckeria,* lateral view of skeleton. (E) *Dinodontosaurus,* lateral view of skeleton. (A) After Ochev; (B) after Bonaparte; (C) after Romer; (D) after von Huene; (E) after Romer. Bar scales: (A, C) 10 cm long; (B) 2 cm long; (D, E) 1 m long.

sodon stahleckeri Huene, *Exaeretodon major* Huene, and *Probelesodon kitchingi* Teixeira.

7.5. Marine cross-correlation

Berdyankian is correlated to the early Ladinian based largely on the age of the Lettenkohle. The Chanarian tetrapods from Argentina are older than late Carnian, which is the age of the overlying tetrapod assemblage from the Ischigualasto Formation. The Chanarian has long been considered Ladinian (e.g., Bonaparte, 1966), but without a strong basis.

7.6. Comments

Berdyankian is difficult to correlate globally, largely because of a paucity of tetrapod assemblages of this age. Two clusters of localities (European and South American) are equated, largely on the basis of the Lettenkohle dicynodont and the conclusion that '*Elephantosaurus*' is a stahleckeriid, possibly a synonym of *Stahleckeria* (Lucas and Wild, 1995). The South American Chanarian LVF thus is the provincial secondary standard correlative to the Berdyankian.

Like the Perovkan, the Berdyankian is relatively long, at least as long as the Ladinian and part of the early Carnian. Nevertheless, Berdyankian vertebrate fossil assemblages probably only represent the earlier part of this time interval. Therefore, the potential exists to recognize another LVF between the Berdyankian and Otischalkian, although data to do this are insufficient at present.

8. Otischalkian LVF

8.1. Definition

Lucas and Hunt (1993b) proposed the Otischalkian LVF, based on the vertebrate fossil assemblage of the Colorado City Member of the Dockum Formation, Chinle Group (Lucas and Anderson, 1993a,b) near the defunct town of Otis Chalk, Howard County, Texas (Lucas et al., 1993, 1997a). I term this the *Paleorhinus* Assemblage Zone. The beginning of the Otischalkian is the FAD of *Paleorhinus*. The end of the Otischalkian is the beginning of the Adamanian, which is defined by the FAD of *Rutiodon*.

8.2. Index fossils

The following tetrapod genera are restricted to Otischalkian time and are widespread and/or common enough to be useful as index fossils: *Paleorhinus*, *Angistorhinus*, *Longosuchus* (= *Lucasuchus*), *Metoposaurus, Doswellia* (Fig. 10).

8.3. Type vertebrate assemblage

The type fauna of the Otischalkian is the assemblage of vertebrate fossils from just north of the defunct town of Otis Chalk in Howard County, Texas. Lucas et al. (1993) recently reviewed the fauna, which is from the Colorado City Member (formerly Iatan Member, see Lucas and Anderson, 1995) of the Dockum Formation of the Chinle Group. The following taxa are present: the temnospondyls *Latiscopus disjunctus* Wilson, *Buettneria perfecta* Case and *Apachesaurus* sp.; a procolophonid; the rhynchosaur *Otischalkia elderae* Hunt and Lucas; the diapsids *Doswellia kaltenbachi* Weems and *Trilophosaurus buettneri* Case; the prolacertiform *Malerisaurus langstoni* Chatterjee; the poposaurid *Poposaurus gracilis* Mehl; the aetosaurs *Longosuchus meadei* (Sawin) (= *Lucasuchus hunti* Long and Murry) and a new aetosaur genus (see Lucas et al., 1993); and the phytosaurs *Paleorhinus bransoni* Williston, *Angistorhinus alticephalus* Stovall and Wharton, and *Brachysuchus megalodon* Case.

8.4. Principal correlatives

Besides Chinle Group correlatives, principal Otischalkian vertebrate assemblages are from the: Sanfordian interval of the Newark Supergroup basins of eastern North America; Schilfsandstein, Kieselsandstein and Blasensandstein of the German Keuper; Irohalene Member (T4) of the Timesgadiouine Formation, Argana Group, Morocco; and basal part of the Maleri Formation, Pranhita–Godavari Valley, India.

Otischalkian principal correlatives and the type fauna encompass a broad geographic range of Chinle Group outcrops in Wyoming, New Mexico, and Texas. They occur in units of the lower part of the Chinle Group that were previously correlated with each other on a lithostratigraphic basis (Lucas, 1993b). The most well-known principal correlative of the type Otischalkian fauna is the vertebrate-fossil assemblage from the Popo Agie Formation of Wyoming, principally Fremont County (see reviews by Colbert, 1957, and Lucas, 1994) and include: the temnospondyl *Buettneria perfecta* Case; an unidentified rhynchosaur (Hunt and Lucas, 1991b); *Paleorhinus bransoni* Williston; *Angistorhinus grandis* Mehl; *Desmatosuchus* sp.; *Poposaurus gracilis* Mehl; *Heptasuchus clarki* Dawley, Zawiskie and Cosgriff; and *Placerias hesternus* Lucas.

A less well known principal correlative is the small assemblage from the Salitral Formation in Rio Arriba County, New Mexico (Lucas and Hunt, 1992). The Salitral assemblage consists of Metoposauridae, *Longosuchus meadei*, Phytosauridae, and an indeterminate dinosaur.

The stratigraphically lower formations of the Deep River, Dan River, Richmond-Taylorsville, Gettysburg, Newark and Fundy basins contain two distinct vertebrate fossil assemblages of late Carnian age. The oldest of these was used by Huber et al. (1993b) as the basis of the Sanfordian LVF, after the type assemblage from the middle Pekin Formation in the Sanford sub-basin of the Deep River basin complex. An age-equivalent assemblage from the middle Wolfville Formation (Fundy basin) is also included in this LVF. The collective fauna of this LVF includes the metoposaurid *Metoposaurus bakeri* (Case), procolophonids, the traversodontid *Arctotraversodon plemmyridon* Hopson, the dicynodont *Placerias hesternus* Lucas, a hyperodapedon-

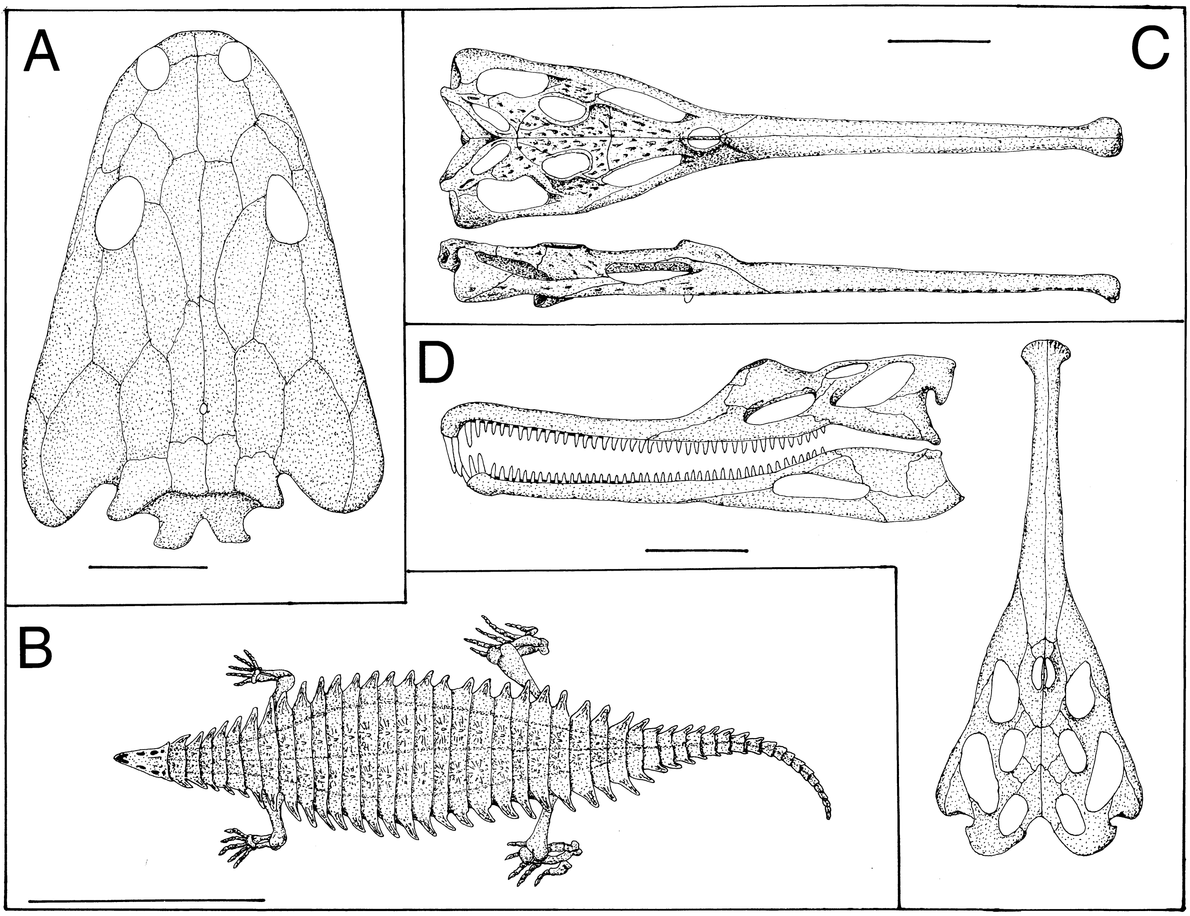


Fig. 10. Some Otischalkian index fossils. (A) *Metoposaurus*, dorsal view of skull. (B) *Longosuchus*, dorsal view of skeleton. (C) *Paleorhinus*, dorsal (above) and lateral (below) views of skull. (D) *Angistorhinus*, lateral (left) and dorsal (right) views of skull. (A) After Hunt; (B) after Lucas and Hunt; (C, D) after Case. Bar scales: (A, C, D) 10 cm long; (B) 1 m long.

tid rhynchosaur (cf. *Scaphonyx*), the aetosaurs *Desmatosuchus* sp. and *Longosuchus meadei* (Sawin), indeterminate rauisuchians (‘*Zamotus*’), indeterminate phytosaur fragments and undescribed, fragmentary dinosaur remains (e.g., Cope, 1871; Olsen et al., 1989; Hunt and Lucas, 1990; Huber et al., 1993a; Hunt, 1993; Sues et al., 1994). The Sanfordian correlates with the Chinle Group Otischalkian LVF (note shared presence of *Metoposaurus bakeri*, *Buettneria*, hyperodapedontid rhynchosaurs, *Desmatosuchus*, *Longosuchus*, *Doswellia*, and *Placerias*).

In Germany, the Schilfsandstein, Kieselsandstein and/or Blasensandstein produce *Metoposaurus* and *Paleorhinus* and thus can be correlated to the Otischalkian (Hunt and Lucas, 1991a).

The 500-m-thick Irohalene Member of the Timesgadiouine Formation (interval T-5 of Dutuit, 1966; Tixeront, 1971) has produced most of the Late Triassic vertebrate fauna from Morocco. It contains the majority of vertebrate localities described by Dutuit (1972, 1976, 1977, 1988, 1989a,b). Most of these occur in the lower part of the member and have produced a moderately diverse fauna that includes the latiscopid temnospondyl *Almasaurus*, the metoposaur *Dutuitosaurus ouazzoui* Hunt, the phytosaur *Paleorhinus*, the dicynodont *Placerias* (= *Moghreberia*, = *Azarifeneria*: Cox, 1991; Lucas and Wild, 1995), at least one ornithischian dinosaur and the prosauropod *Azendohsaurus laaroussii* Dutuit (see Gauffre, 1993). Several localities of Dutuit (1976) occur in the upper part of the Irohalene Member, and may represent a distinct faunal horizon that includes the metoposaur *Arganasaurus lyazidi* (Dutuit), a large phytosaur of undetermined affinity, the phytosaur *Angistorhinus*, and the dicynodont *Placerias*. The presence of *Paleorhinus*, *Angistorhinus* and *Placerias* supports assigning the Irohalene Member tetrapod assemblage(s) an Otischalkian age.

In the Pranhita–Godavari Valley of India, the basal Maleri Formation produces a tetrapod assemblage that includes the temnospondyl *Metoposaurus maleriensis*, the rhynchosaur *Paradapedon huxleyi* (Lydekker), the phytosaur *Paleorhinus* (= *Parasuchus*) *hislopi* (Lydekker), the protorosaur *Malerisaurus*, an aetosaur, the theropod dinosaur *Alwalkeria maleriensis* (Chatterjee), a prosauropod (‘cf. *Massospondylus*’ of Kutty and Sengupta, 1989), a large dicynodont, and the cynodont *Exeraetodon statisticae* Chatterjee (e.g., von Huene, 1940; Roychowdhury, 1965; Chatterjee, 1967, 1974, 1978, 1980, 1982, 1987; Chatterjee and Roychowdhury, 1974). This is the only well-described assemblage from the Pranhita–Godavari Valley. It includes *Paleorhinus* and *Metoposaurus*, taxa characteristic of Otischalkian-age strata of the Chinle Group.

8.5. Marine cross-correlation

The following evidence indicates that the Otischalkian is of Carnian (late Julian–early Tuvalian) age on the SGCS.

(1) *Paleorhinus* is known from Tuvalian marine strata in Austria (Hunt and Lucas, 1991a). Its nonmarine occurrences in India and Germany are also considered by various lines of evidence to be of late Carnian age. *Paleorhinus* thus provides an important cross-correlation between marine and nonmarine Triassic biochronologies.

(2) *Metoposaurus* is known only from early or late Carnian localities outside of North America (Hunt, 1993).

(3) Palynostratigraphy assigns a late Carnian age to the lower Chinle Group, including the strata of Otischalkian age, and an early Carnian age to the oldest Sanfordian strata of the Newark Supergroup (Litwin et al., 1991, 1993; Cornet, 1993).

(4) Sequence stratigraphy of the Chinle Group advocated by Lucas (1991, 1993b), Lucas and Marzolf (1993) and Lucas and Huber (1994) assigns lower Chinle Group strata to a single sequence, the Shinarump–Blue Mesa sequence. This sequence correlates well to a late Carnian marine sequence in Nevada (Lucas and Huber, 1994).

(5) Magnetostratigraphy correlates lower Chinle Group strata to the late Carnian portion of the Newark Supergroup magnetostratigraphy (Kent et al., 1995; Molina-Garza et al., 1996).

9. Adamanian LVF

9.1. Definition

Lucas and Hunt (1993b) based the Adamanian LVF on the vertebrate fauna of the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, Arizona (Lucas, 1993c; Lucas and Hunt, 1993b; Lucas et al., 1997a). I term this the *Rutiodon* Assemblage Zone. The beginning of the Adamanian is defined as the FAD of *Rutiodon*. The end of the Adamanian is the beginning of the Revueltian, which is defined by the FAD of *Pseudopalatus*.

9.2. Index fossils

The following tetrapod genera are restricted to Adamanian time and are widespread and/or common enough to be useful as index fossils: *Scaphonyx*, *Stagonolepis* and *Rutiodon*-grade phytosaurs, including *Leptosuchus* and *Smilosuchus* (Fig. 11).

9.3. Type assemblage

The type fauna of the Adamanian is the assemblage of vertebrate fossils found in the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, near the defunct railroad siding of Adamana, Arizona. Recent faunal lists have been provided by Murry and Long (1989) and Long and Murry (1995). The fauna includes the following tetrapods: the temnospondyls *Apachesaurus gregorii* Hunt and *Buettneria perfecta* Case; the aetosaurs *Desmatosuchus haplocerus* Case (= *Acaenasuchus geoffreyi* Long and Murry), *Stagonolepis wellesi* (Long and Ballew), and *Paratypothorax andressi* Long and Ballew; the phytosaurs *Rutiodon*

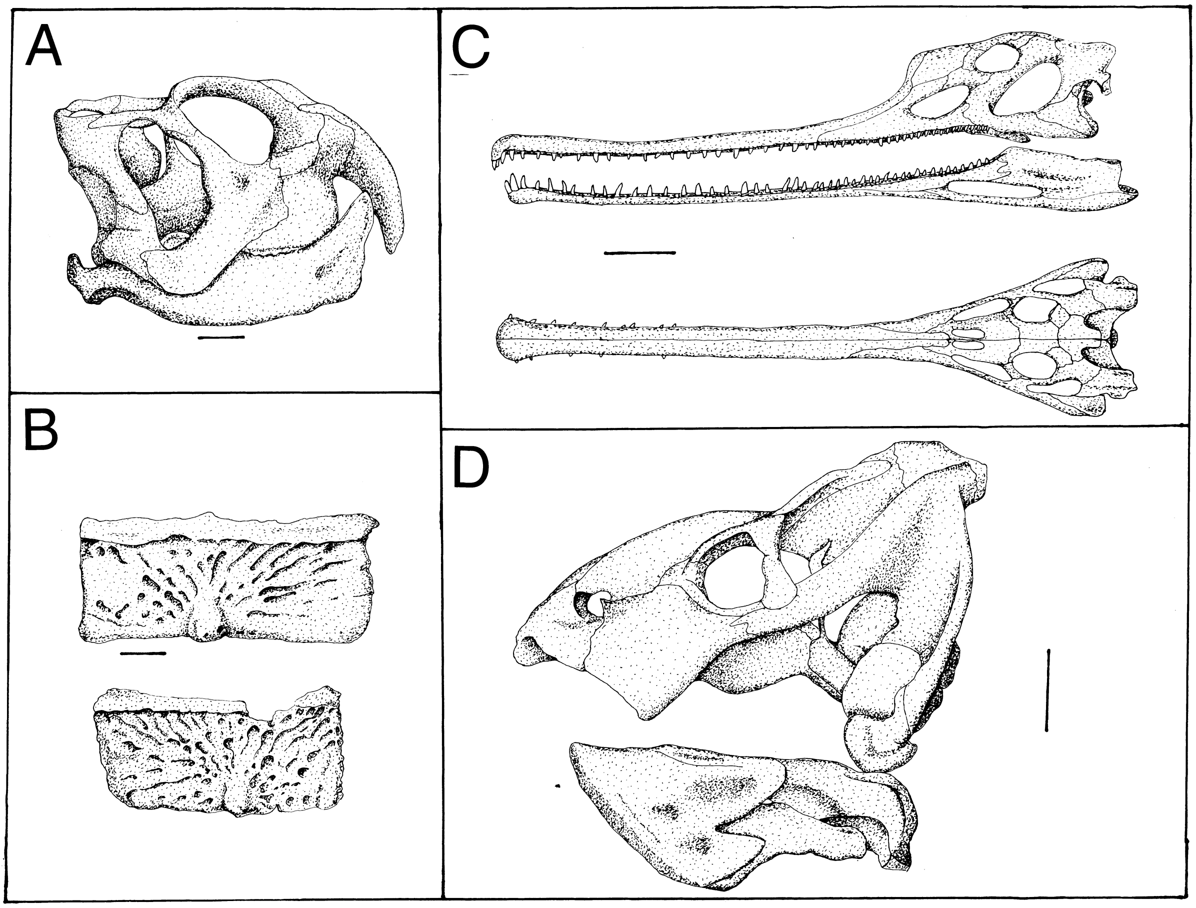


Fig. 11. Some Adamanian index fossils. (A) *Scaphonyx*, lateral view of skull and lower jaw. (B) *Stagonolepis*, dorsal view of paramedian plates. (C) *Rutiodon*, lateral (above) and dorsal (below) views of skull and lower jaw. (D) *Ischigualastia*, lateral view of skull and lower jaw. (A) After Romer; (B) after Long and Ballew; (C) after Case; (D) after Cox. Bar scales: (C, D) 10 cm long; (A) 1 cm long; (B) 3 cm long.

spp. (I follow Ballew (1989) and Hunt (1994) in considering *Leptosuchus* a junior subjective synonym of *Rutiodon*) and *Smilosuchus* Long and Murry; the rauisuchians *Postosuchus kirkpatricki* Chatterjee and *Chatterjeea elegans* Long and Murry; the ?sphenosuchians *Hesperosuchus agilis* Colbert and *Acallosuchus rectori* Long and Murry; the diapsids *Parrishea* sp. and *Vancleavea campi* Long and Murry; and the dicynodont *Placerias hesternus* Lucas.

9.4. Principal correlatives

Besides the Chinle Group correlatives, major Adamanian faunas are those of the Conewagian interval of the Newark Supergroup basins of eastern North America, Lossiemouth Sandstone Formation, Scotland, Ischigualasto Formation, Argentina, and upper Santa Maria Formation, Brazil.

In the Chinle Group, Adamanian vertebrates are widespread and include: the vertebrate fossil assemblages of the *Placerias* and Downs' quarries, Bluewater Creek Formation, Arizona; fauna from the Bluewater Creek Formation and Blue Mesa Member of the Petrified Forest Formation, McKinley and Cibola counties, New Mexico (Heckert, 1997); faunas from the Los Esteros and Tres Lagunas members, Santa Rosa Formation, vicinity of Lamy, Santa Fe County, New Mexico (Hunt and Lucas, 1995);

Garita Creek Formation, Santa Rosa and vicinity, Guadalupe County, New Mexico (Hunt et al., 1989; Hunt and Lucas, 1993a); and Tecovas Formation, West Texas (Murry, 1989).

The fauna at the *Placerias* and Downs' quarries has most recently been discussed by Kaye and Padian (1994) and Long and Murry (1995). The following list is derived from both those sources and from Lucas et al. (1997a): *Buettneria perfecta* Case; *Apachesaurus gregorii* Hunt; *Chinleogomphius jacobsi* Murry; *Acallosaurus rectori* Long and Murry; *Placerias hesternus* Lucas; *Tanytrachelos* sp.; *Trilophosaurus* sp.; *Rutiodon*/*Leptosuchus*; *Paleorhinus* sp.; *Stagonolepis wellesi* (Long and Ballew), and/or *Stagonolepis robertsoni* Agassiz; *Desmatosuchus haplocerus* Case; *Acaenasuchus geoffreyi* Long and Murry; *Postosuchus kirkpatricki* Chatterjee; *Poposaurus gracilis* Mehl; *Chatterjeea elegans* Long and Murry; *Hesperosuchus agilis* Colbert; *Tecovasaurus murryi* Hunt and Lucas; cf. *Uatchitodon*; and an indeterminate ceratosaur.

Hunt and Lucas (1993a) summarized the Triassic paleontology and biochronology of New Mexico. They noted the presence of the following taxa from the Los Esteros Member, Santa Rosa Formation, near Lamy, New Mexico: *Apachesaurus* sp.; *Trilophosaurus* sp.; *Rutiodon* sp.; *Angistorhinus* sp.; *Desmatosuchus* sp.; *Stagonolepis* sp.; cf. *Ischigualastia* sp.; and several new genera of archosaurs, including at least one new aetosaur (Hunt and Lucas, 1993a). The overlying Garita Creek Formation contains the following taxa: *Buettneria perfecta* Case; indeterminate metoposaurids, phytosaurs, and rauisuchians; cf. *Desmatosuchus* sp.; *Paratypothorax* sp.; and an indeterminate aetosaur previously misidentified as *Typothorax* sp.

The Tecovas Formation of West Texas contains the following taxa: *Buettneria perfecta* Case; *Apachesaurus gregorii* Hunt; *Trilophosaurus* sp.; *Rutiodon* (= *Leptosuchus*) *crosbiensis* (Case); *Smilosuchus gregorii* Camp; *Desmatosuchus haplocerus* Case; *Stagonolepis wellesi* (Long and Ballew); *Postosuchus kirkpatricki* Chatterjee; *Parrishea mccreai* Long and Murry; and *Adelobasileus cromptoni* Lucas and Hunt (Lucas et al., 1994a).

In the Deep River basin of North Carolina, an assemblage of the Conewagian LVF from the Cumnock Formation is superposed on the type Sanfordian assemblage. Conewagian assemblages are defined by the type occurrence in the middle New Oxford Formation along Conewago Creek in south-central Pennsylvania (Gettysburg basin: Huber et al., 1993b; Sullivan et al., 1995; Lucas and Sullivan, 1997) and also are known from the Cow Branch Formation (Dan River basin), and upper Stockton and Lockatong formations (Newark basin). The most widespread and characteristic Conewagian tetrapod is the phytosaur *Rutiodon carolinensis* Emmons, which co-occurs with the metoposaur *Buettneria perfecta* Case, archosaurs of uncertain affinity, an aetosaur (*Desmatosuchus* cf. *D. haploceras* Case), one or more ornithischians (e.g., *Pekinosaurus olseni* Hunt and Lucas and *Galtonia gibbidens* [Cope]), the archosaur *Tanytrachelos ahynis* Olsen and the lepidosauromorph *Icarosaurus siefkeri* Colbert (e.g., Emmons, 1856; Olsen, 1980; Olsen et al., 1989; Sues, 1992; Huber et al., 1993a; Hunt, 1993; Hunt and Lucas, 1994; Doyle and Sues, 1995). Conewagian assemblages correlate with the Adamanian LVF of the Chinle Group, based on the shared presence of *Buettneria perfecta*, *Rutiodon* and other *Rutiodon*-grade phytosaurs (*Smilosuchus* of Long and Murry, 1995), *Desmatosuchus* and broadly similar ornithischian dinosaurs (e.g., Murry and Long, 1989; Lucas et al., 1992, 1997a; Huber et al., 1993b; Hunt, 1993; Hunt and Lucas, 1994 for documentation of the Chinle Group records).

The tetrapod assemblage of the Lossiemouth Sandstone Formation of Grampian (Elgin) Scotland comes from small quarry workings and the coastal section at Lossiemouth. Benton and Spencer (1995) (pp. 62–72) provided a detailed summary and indicate that all sites come from a narrow stratigraphic range, so I treat the vertebrates as a single biostratigraphic assemblage. It includes the procolophonid *Leptopleuron lacertinum* Owen, the sphenodontid *Brachyrhinodon taylori* Huene, the rhynchosaur *Hyperodapedon gordoni* Huxley, the aetosaur *Stagonolepis robertsoni* Agassiz, the ornithosuchids *Ornithosuchus longidens* (Huxley) (= *O. woodwardi* Newton: Walker, 1964), the crocodylomorph *Erpetosuchus granti* Newton, the probable ornithodiran *Scleromochlus taylori* Woodward, and the 'dinosaur' *Saltopus elginensis* Huene. The presence of *Stagonolepis* supports correlation of this assemblage to the Chinle Group Adamanian.

In Argentina, the Ischigualasto Formation is 500 to 900 m thick and consists of drab mudstones, tuffs and sandstones that produce an extensive tetrapod assemblage including: the temnospondyl *Promastodonosaurus bellmanni* Bonaparte; the chiniquodontid cynodont *Chiniquodon* sp., the gomphodont cynodonts *Exaraetodon frenguellii* Cabrera, *Proexaraetodon vincei* Bonaparte, and *Ischignathus sudamericanus* Bonaparte; the dicynodont *Ischigualastia jenseni* Cox; the pseudosuchians *Saurosuchus galilei* Reig and *Proterochampsa barrionuevoi* Reig; the aetosaur *Stagonolepis* (= *Aetosauroides*); the rhynchosaur *Scaphonyx sanjuanensis* Sill; and the dinosaurs *Herrerasaurus* (= *Ischisaurus*? = *Frenguellisaurus*), *Eoraptor* and *Pisanosaurus* (e.g., Cabrera, 1944; Reig, 1959, 1961, 1963; Casamiquela, 1960, 1962; Cox, 1965; Bonaparte, 1976; Rogers et al., 1993; Sereno et al., 1993). The assemblage slightly overlaps and mostly overlies the Herr Toba bentonite that yielded a ^{40}Ar/^{39}Ar age of 227.8 ± 0.3 Ma (Rogers et al., 1993).

Romer (1960, 1962a,b) and Reig (1961, 1963) assigned the Ischigualasto tetrapods a Middle Triassic (Ladinian) age. This well fitted the concept — developed and best articulated by Romer — that Middle Triassic tetrapod assemblages have numerous gomphodont cynodonts and an ‘explosive development’ of rhynchosaurs. However, Bonaparte (1966, 1967), noting that rhynchosaurs co-occur with phytosaurs and aetosaurs in the Upper Triassic of Europe and India, assigned a Carnian age to the Ischigualasto vertebrate assemblage.

Subsequent workers have accepted the Carnian age assignment but have correlated the Ischigualasto tetrapods as early or ‘middle’ Carnian, arguing that they predate late Carnian assemblages such as the basal Chinle or lower Maleri, etc. Therefore, according to common practice, the dinosaur fossils from the Ischigualasto Formation are considered to be the oldest known (e.g., Benton, 1990; Rogers et al., 1993; Novas, 1996).

Hunt and Lucas (1991a,b), Lucas et al. (1992) and Lucas and Hunt (1993a) challenged this practice, arguing that the Ischigualasto Formation is of late Carnian age based on: (1) postcrania identified as cf. *Ischigualastia* sp. from Adamanian-aged strata of the Chinle Group, suggesting an Adamanian–Ischigualastian correlation; (2) the presence of *Staurikosaurus*-like dinosaurs in the Adamanian interval of the Chinle Group; and (3) presence of rhynchosaurs in late Carnian strata of the Chinle Group, Newark Supergroup, Lossiemouth Sandstone Formation and Maleri Formation. Although rhynchosaurs are not abundant in any of these strata, their presence refutes Romer’s assertion that rhynchosaurs indicate a Middle Triassic age.

None of these arguments are incontrovertible evidence for a late Carnian age of the Ischigualasto tetrapods. However, recent revision of the South American aetosaurs by Heckert and Lucas (1996) indicates that *Aetosauroides* from Argentina and Brazil is a junior subjective synonym of the Adamanian index fossil *Stagonolepis*. This strongly supports an Adamanian correlation of the Ischigualasto tetrapods.

In Brazil, the principal Upper Triassic vertebrate assemblage from the Santa Maria Formation is from the vicinity of Santa Maria City. This is the Rhynchocephalia assemblage zone of Barberena (1977) or the *Scaphonyx* assemblage of Barberena et al. (1985), from the upper part of the Santa Maria Formation. The assemblage consists of: abundant fossils of the rhynchosaur *Scaphonyx fischeri* Smith-Woodward and the aetosaur ‘*Aetosauroides*’; less abundant traversodontids, including *Therioherpeton cargnini* Bonaparte and Barberena (possibly a chiniquodontid) and *Gomphodontosuchus brasiliensis* Huene; the proterochampsids *Cerritosaurus binsfeldi* Price, *Rhadinosuchus gracilis* Huene and *Hoplitosuchus raui* Huene; the archetypal rauisuchian *Rauisuchus tiradentes* Huene; and the primitive dinosaur *Staurikosaurus pricei* Colbert. Clearly, the presence of *Scaphonyx* and ‘*Aetosauroides*’ supports correlation with the vertebrates of the Ischigualasto Formation in Argentina, and therefore an Adamanian (= Ischigualastian) age.

In the Pranhita–Godavari Valley of India, the upper vertebrate fossil assemblage from the Maleri Formation is stratigraphically above the lower assemblage, but its stratigraphic range is not clear. This upper assemblage includes an aetosaur, prosauropods and a large dicynodont. Chigutisaurid amphibians (*Compsocerops cosgriffi* and *Kuttycephalus triangularis*: Sengupta, 1995) and a ‘*Rutiodon*-like’ phytosaur are also present. Therefore, this assemblage may be Adamanian, but needs further documentation.

9.5. Marine cross-correlation

The Adamanian is of latest Carnian age based on palynostratigraphy, sequence stratigraphy and magnetostratigraphy (see references cited above under Section 8.5). In West Texas, Otischalkian and Adamanian tetrapod assemblages are stratigraphically superposed (Lucas, 1993b; Lucas and Anderson, 1993a,b, 1994, 1995; Lucas et al., 1993, 1994a). Therefore, Adamanian time is a younger portion of the Tuvalian than the Otischalkian. Norian (Revueltian LVF) vertebrates are stratigraphically above Adamanian vertebrates in Arizona, New Mexico and Texas. Therefore, Adamanian vertebrates are the youngest Carnian vertebrates known.

9.6. Comment

Like the Otischalkian, the Adamanian is relatively short, easily recognized over a broad area and relatively precisely correlated to the SGCS.

10. Revueltian

10.1. Definition

Lucas and Hunt (1993b) introduced the term Revueltian LVF to refer to the time equivalent to the vertebrate fossil assemblage of the Bull Canyon Formation in east-central, New Mexico, USA (Lucas et al., 1985; Hunt, 1994; Hunt and Lucas, 1997). I term this the *Pseudopalatus* Assemblage Zone. The name of the LVF is for Revuelto Creek, one of the key collecting areas in eastern New Mexico. Revueltian time begins with the FAD of the phytosaur *Pseudopalatus*. The end of the Revueltian is the beginning of the Apachean, which is defined by the FAD of the phytosaur *Rendondasaurus*.

10.2. Index fossils

The following tetrapod taxa are restricted to Revueltian time and are widespread and/or common enough to be useful as index fossils: *Typothorax*, *Aetosaurus* and *Pseudopalatus*-grade phytosaurs (Fig. 12).

10.3. Type vertebrate assemblage

The type assemblage of the Revueltian is that of the Bull Canyon Formation in east-central New Mexico (Quay and Guadalupe counties), and is called the *Pseudopalatus* Assemblage Zone. The following taxa are present: the metoposaurid *Apachesaurus gregorii* Hunt; the phytosaurs *Pseudopalatus pristinus* Mehl and *P. andersoni* (Mehl); the aetosaurs *Desmatosuchus* sp., *Paratypothorax* sp., *Typothorax coccinarum* Cope, and *Aetosaurus arcuatus* (Marsh); the dinosaurs *Revueltosaurus callenderi* Hunt and *Lucianosaurus wildi* Hunt and Lucas; the rauisuchians *Chatterjeea elegans* Long and Murry and *Postosuchus kirkpatricki* Chatterjee; the aberrant thecodonts *Shuvosaurus inexpectans* Chatterjee and *Hesperosuchus* sp.; and the cynodont *Pseudotriconodon chatterjeei* Lucas and Oakes (cf. Hunt, 1994).

10.4. Principal correlatives

Besides Chinle Group correlatives, the principal Revueltian tetrapod assemblages are those of the Newark Supergroup of eastern North America of Neshanician and Cliftonian (part) age, Ørsted Dal Member of the Fleming Fjord Formation, Greenland, Stubensandstein and Knollenmergel of the German Keuper, Zorzino Limestone and Forni Dolomite, northern Italy, and lower part of Dharmaran Formation, India.

The provincial Neshanician LVF is based on a limited fossil assemblage typified by the aetosaur *Aetosaurus arcuatus* (Marsh, 1896) (Lucas et al., 1996, 1998a). This taxon is present in 'Lithofacies Association II' of the Chatham Group (Durham sub-basin of the Deep River basin), the Newark basin (range zone: Warford through Neshanic members of the lower Passaic Formation), and the Hartford Group of central Connecticut (middle New Haven Formation). Other vertebrates from the Neshanician LVF include indeterminate metoposaurid and phytosaur teeth, skull and scute fragments (e.g., '*Belodon validus*' Marsh, 1893), an undescribed rauisuchian, crocodylomorph and traversodontid (from 'Lithofacies Association II': P. Olsen, pers. commun., 1995), a crocodylomorph skull and a sphenodontid premaxilla (lower New Haven Formation) and a dominance of the primitive neopterygian *Semionotus* sp. over

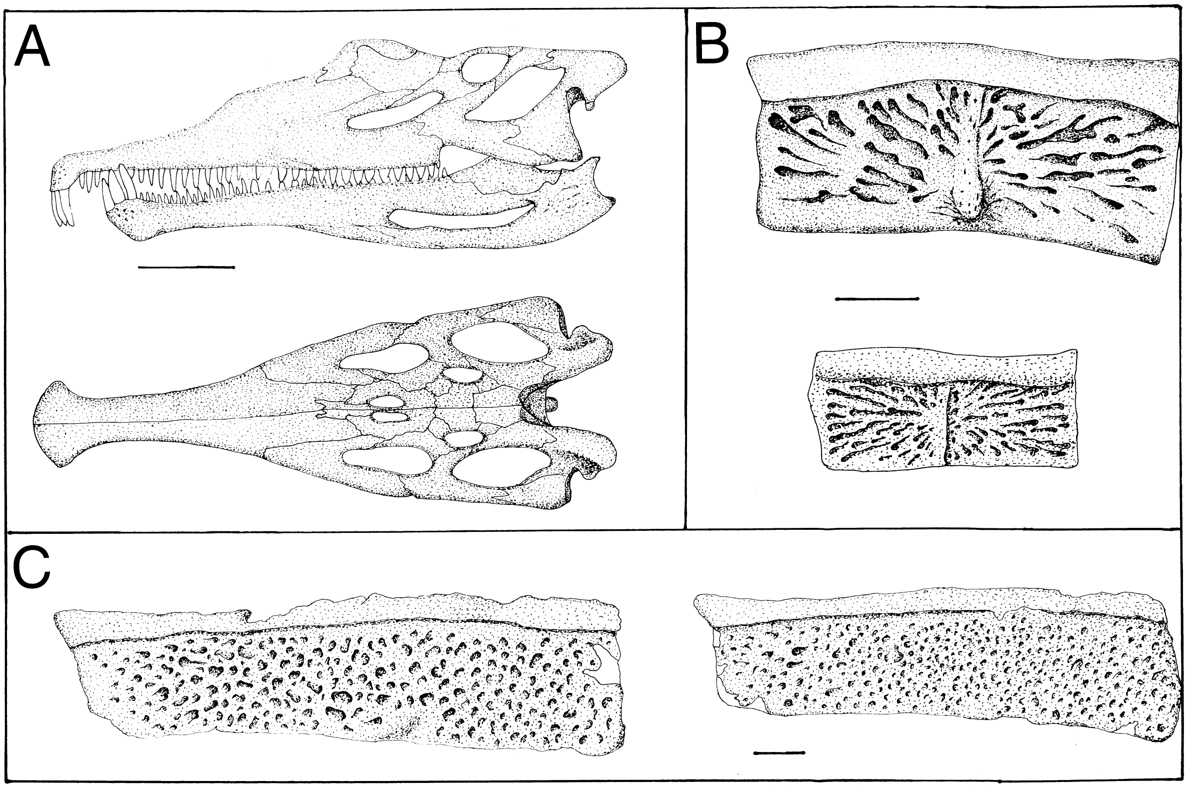


Fig. 12. Some Revueltian index fossils. (A) *Pseudopalatus*, lateral (above) and dorsal (below) views of skull. (B) *Aetosaurus*, dorsal view of paramedian plates. (C) *Typothorax*, dorsal view of paramedian plates. (A) After Case; (B) after Wild; (C) after Long and Ballew. Bar scales: (A) 10 cm long; (B) 1 cm long; (C) 3 cm long.

other fish taxa, a trend also apparent in age-equivalent strata of the Chinle Group and German Keuper (Huber et al., 1993c).

The Cliftonian LVF is based on a low-diversity assemblage defined by the distribution of the procolophonid *Hypsognathus fenneri* Gilmore, 1928. This taxon is common in the type area, from the middle (?Mettlars Member) to the upper (?Member TT) Passaic Formation of the northern Newark basin (e.g., Baird, 1986). It is also known from the upper New Haven Formation of the Hartford basin, central Connecticut, and the basal Blomidon Formation in the Fundy basin, Nova Scotia (Sues et al., 1997). The Fundy basin specimen of *Hypsognathus* was obtained from pebble conglomerate at the base of the Blomidon Formation, which unconformably overlies the Wolfville Formation. The only other vertebrates that occur in the interval of Cliftonian age are indeterminate phytosaur remains (including the holotype of ‘*Clepsysaurus pennsylvanicus*’ Lea, 1851) from the Ukrainian Member of the Passaic Formation in the Newark basin, moderately diverse tetrapod footprint assemblages at many horizons in the Passaic Formation (Szajna and Silvestri, 1996), and an indeterminate sphenodontid from the upper New Haven Formation (Olsen, 1980; Sues and Baird, 1993).

The Malmos Klint and overlying Ørsted Dal members of the Fleming Fjord Formation in eastern Greenland produce fossil vertebrates of Late Triassic age (Jenkins et al., 1994). The Malmos Klint Member has produced fragmentary fossils of plagiosaurids, the cyclotosaur *Cyclotosaurus*, possible phytosaur fragments and the prosauropod dinosaur *Plateosaurus*. The Ørsted Dal Member assemblage is much more diverse, i.e., coelacanth fishes, ?*Saurichthys*, a lungfish, the plagiosaurid *Gerrothorax* cf. *G. pulcherrimus* Fraas, the cyclotosaur *Cyclotosaurus* cf. *C. posthumus* Fraas, the turtle cf. *Proganochelys* sp., unidentified sphenodontians, the aetosaurs *Aetosaurus ferratus* Fraas and *Paratypothorax andressi* Long and Ballew, a pterosaur, the prosauropod dinosaur *Plateosaurus engelhardti* Meyer, a theropod dinosaur, theropod dinosaur footprints (*Grallator* sp.), and the mammals *Kuehneotherium* sp., cf. *Brachyzostrodon*? and *Haramiyavia clemmenseni* Jenkins, Gatesy, Shubin and Amaral (also see Jenkins et al., 1997). As Jenkins et al. (1994) argued, this assemblage shares many taxa with the German Stubensandstein. More specifically, other than *Plateosaurus*, most taxa from the Ørsted Dal Member are known in the lower Stubensandstein, to which I correlate the Greenland assemblage.

In Germany, the best known and most diverse Keuper tetrapod assemblage is that of the lower Stubensandstein. This assemblage includes the temnospondyls *Cyclotosaurus* and *Gerrothorax*, the earliest turtles (*Proganochelys* and *Proterochersis*), *Pseudopalatus*-grade phytosaurs (*Nicrosaurus*), the aetosaurs *Aetosaurus* and *Paratypothorax*, rauisuchians (*Teratosaurus*), theropod dinosaurs, and the prosauropods *Sellosaurus* and *Thecodontosaurus* (see Benton, 1993, for bibliography). The phytosaurs, aetosaurs, and rauisuchians provide a strong basis for a Stubensandstein–Revueltian correlation (Lucas and Hunt, 1993b; Hunt, 1994). The younger, middle and upper Stubensandstein, produce a similar, but less diverse assemblage, so I also correlate them to the Revueltian. Whether or not the lowest occurrence of *Mystriosuchus* in the middle Stubensandstein is of biochronologic significance is not clear. The assemblages of the upper Stubensandstein and Knollenmergel are almost entirely dinosaurian — 95% or more of the fossils are of dinosaurs (Benton, 1986, 1991). This contrasts sharply with the lower and middle Stubensandstein assemblages, in which dinosaurs are a much smaller percentage of the fossils collected. However, I regard this change to dinosaur domination as largely a local facies/taphonomic effect, not necessarily a biochronologically significant event (Hunt, 1991).

In the Lombardian Alps of northern Italy, after the regional progradation of platform carbonates during the early–middle Norian (Dolomia Principale), extensional tectonism produced intraplatform depressions occupied by patch reefs, turbiditic debris flows and lagoonal to freshwater facies (Jadoul, 1985; Jadoul et al., 1994). Ammonoid, conodont and palynological biostratigraphy provide direct age control of these deposits, which are assigned to the Zorzino Limestone and the Forni Dolomite. The Zorzino Limestone (Calcare de Zorzino) is very close in age to the Alaunian–Sevatian boundary. It can be correlated to the younger part of the *Himavatites columbianus* Zone (Jadoul et al., 1994; Roghi et al., 1995). Tetrapods from this unit at the Cene and Endenna quarries (Wild, 1989; Pinna, 1993) in Lombardy are: the diapsids *Endennasaurus acutrirostris* Renesto and ‘*Vallesaurus cenensis*’ Wild; the prolacertiform *Longobardisaurus pandolfii* Pinna; the drepanosaurids *Drepanosaurus unguicaudatus* Pinna and *Megalancosaurus preonensis* Calzavara, Muscio and Pinna; a phytosaur skull assigned to *Mystriosuchus* cf. *M. planirostris* Meyer by Pinna (1993); the aetosaur *Aetosaurus ferratus* Fraas; a new species of *Macrocnemus*; the pterosaurs *Eudimorphodon ranzii* Zambelli and *Peteinosaurus zambellii* Wild; and the placodont *Psephoderma alpinum* Meyer. In Germany, *Mystriosuchus* is well known from the middle Stubensandstein and *Aetosaurus* from the lower–middle Stubensandstein. The age of their Italian records — which represent a point in time, not their entire temporal ranges — is consistent with assigning a middle Norian age to the middle Stubensandstein.

The other Italian Late Triassic tetrapod sites are in the Forni Dolomite (Dolomia di Forni) in the Veneto Prealps of northeastern Italy. These strata are of middle–late Alaunian (*Himavatites columbianus* Zone) age as well, based on conodonts (Roghi et al., 1995). They produce the drepanosaurids *Drepanosaurus unguicaudatus* and *Megalancosaurus preonensis*, and the pterosaurs *Eudimorphodon rosenfeldi* Dalla Vecchia, *Eudimorphodon* sp. and *Preonodactylus buffarinii* Wild (Dalla Vecchia, 1995). However, other than *Eudimorphodon*, the tetrapods are endemic and of no biostratigraphic significance.

Upper Triassic tetrapod assemblages from the Indian Subcontinent come from the Pranhita–Godavari Valley of south-central India. Several summaries (Jain et al., 1964; Kutty, 1969; Kutty and Roychowdhury, 1970; Sengupta, 1970; Jain and Roychowdhury, 1987; Yadigiri and Rao, 1987; Kutty et al., 1988; Kutty and Sengupta, 1989; Bandyopadhyay and Roychowdhury, 1996) have been published, but other than the lower Maleri assemblage (see above), relatively few of the fossils have been adequately documented in print, forcing me to rely largely on unsubstantiated genus-level identifications to evaluate the ages of the tetrapod assemblages of Late Triassic age. A case in point is the Dharmaram Formation, which produces two stratigraphically discrete vertebrate fossil assemblages (lower and upper). The stratigraphic range of the lower assemblage has not been published, and it includes a phytosaur that Kutty and Sengupta (1989), in their table 2, list as *Nicrosaurus*, aetosaurs, including a so-called '*Paratypothorax*-like' form, and prosauropod dinosaurs. Based primarily on the *Nicrosaurus* record, I consider the lower assemblage of the Dharmaram Formation a probable Revueltian correlative.

10.5. Marine cross-correlation

Palynostratigraphy, magnetostratigraphy and sequence stratigraphy suggests that the type Revueltian assemblage is of Norian age (Lucas, 1997). Based on stratigraphic position (Huber et al., 1993b; Lucas and Huber, 1993), magnetostratigraphy (Witte et al., 1991; Kent et al., 1995), and palynomorphs (Cornet, 1977), the Neshanician LVF is of early to middle Norian age. Stratigraphic position (Huber et al., 1993b; Lucas and Huber, 1993), magnetostratigraphy (Witte et al., 1991; Kent et al., 1995), and palynomorphs (Cornet, 1977; Fowell and Olsen, 1993) indicate the Cliftonian LVF is of late Norian–Rhaetian age. The Italian records of *Aetosaurus* provide direct evidence that at least part of the Revueltian = middle Norian (Alaunian). I consider Revueltian to correlate approximately with the entire Norian, which is consistent with the evidence cited above (Lucas, 1997). However, whether or not the beginning and end of the Revueltian and Norian are exact equivalents is unclear.

10.6. Comments

By any recent Triassic numerical time scale (e.g., Harland et al., 1990; Gradstein et al., 1995; Kent et al., 1995; Gradstein and Ogg, 1996) the duration of the Norian is at least 10 million years. This means that the Revueltian is one of the longest Triassic LVFs recognized here. It merits subdivision, as Hunt and Lucas (1993c) suggested, perhaps along the lines of the Cliftonian–Neshanician subdivision used in the Newark Supergroup, but no subdivision is attempted here.

11. Apachean

11.1. Definition

Lucas and Hunt (1993b) introduced the term Apachean LVF to refer to the time equivalent to the vertebrate fossil assemblage of the Redonda Formation (Chinle Group) in east-central New Mexico, USA (Lucas et al., 1985; Hunt, 1994; Hunt and Lucas, 1997). I term this the *Redondasaurus* Assemblage Zone. Apachean time begins with the FAD of the phytosaur *Redondasaurus*. The end of Apachean time is the FAD of the crocodylomorph *Protosuchus*.

11.2. Index fossils

The following tetrapod genera are restricted to Apachean time and are widespread and/or common enough to be useful as index fossils: *Redondasaurus*, *Redondasuchus*, *Riojasaurus* (Fig. 13).

11.3. Type vertebrate assemblage

The type assemblage of the Apachean LVF is from the Redonda Formation of the Chinle Group in Guadalupe and Quay Counties, New Mexico, USA. The following taxa are present: the metoposaurid *Apachesaurus gregorii* Hunt, a sphenodontid, a procolophonid; the phytosaurs *Redondasaurus bermani* Hunt and Lucas and *R. gregorii* Hunt and Lucas; the aetosaur *Redondasuchus reseri* Hunt and Lucas; a sphenosuchian; a rauisuchian; a large aetosaur; theropods; and a cynodont? (Hunt and Lucas, 1993b, 1997; Hunt, 1994).

11.4. Principal correlatives

Principal correlatives of the type Apachean assemblage are the Whitaker quarry in the Rock Point Formation of the Chinle Group at Ghost Ranch, New

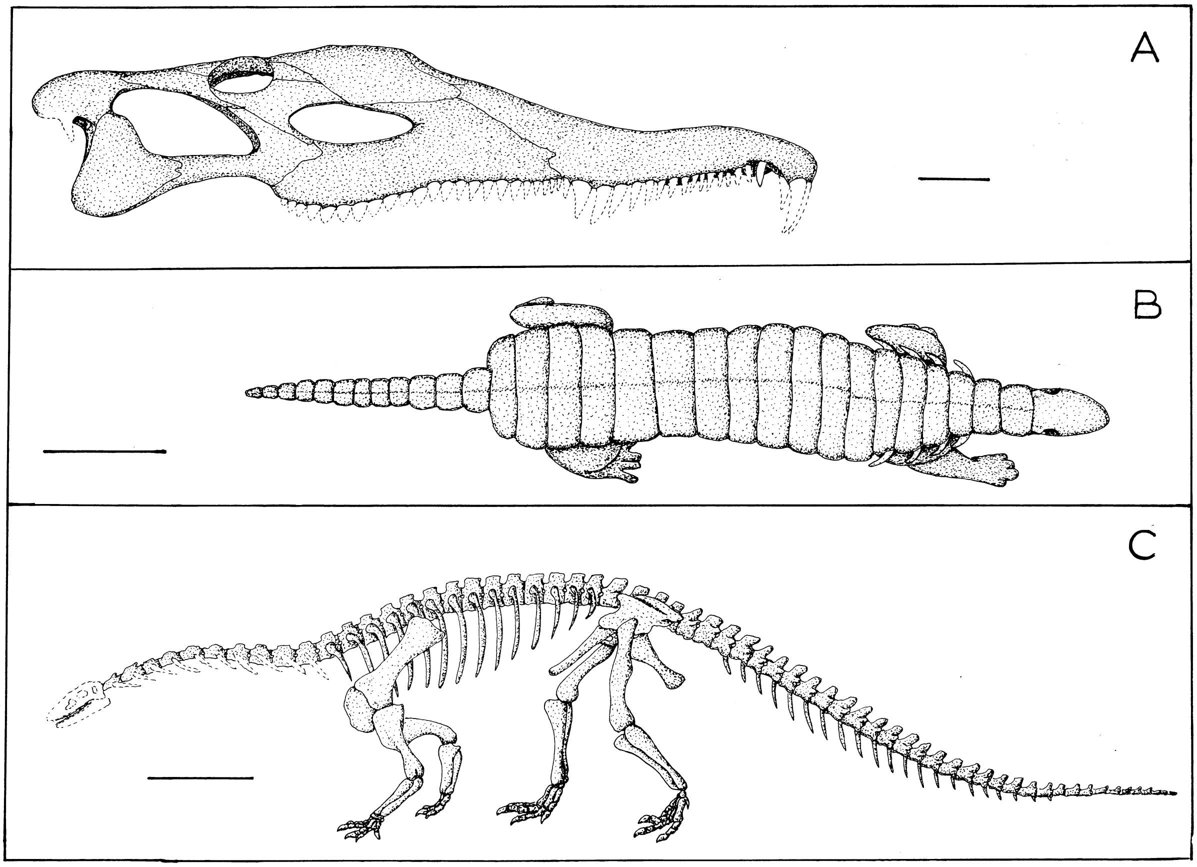


Fig. 13. Some Apachean index fossils. (A) *Redondasaurus*, lateral view of skull. (B) *Redondasuchus*, dorsal view of restoration. (C) *Riojasaurus*, lateral view of skeleton. (A) After Camp; (B) after Heckert et al.; (C) after Bonaparte. Bar scales: (A) 10 cm long; (B) 20 cm long; (C) 50 cm long.

Mexico, the Cliftonian LVF assemblages, in part, of the Newark Supergroup and the Coloradan LVF of Argentina. Some of the fissure fill assemblages in the uppermost Mercia Mudstone Group and/or lowermost Penarth Group of the United Kingdom (Benton and Spencer, 1995) may be Apachean correlatives. However, their ages are problematic, in part, because they lack identifiable phytosaurs, aetosaurs or metoposaurs. Some of the so-called Rhaetian vertebrate sites in France, such as Saint-Nicolas-de-Port, may be Apachean correlatives as well (Lucas and Huber, 1998).

In New Mexico, the Whitaker quarry produces numerous skeletons of the theropod *Coelophysis* (= *Rioarribasaurus*) *bauri* (Cope), the phytosaur *Redondasaurus*, and undescribed rauisuchians and a sphenosuchian (Hunt and Lucas, 1993a).

In Argentina, the Los Colorados Formation consists of siliciclastic red beds approximately 800 m thick. Near its base, a single tetrapod fossil — a dicynodont skull, the holotype of *Jachaleria colorata* Bonaparte 1970 — was collected. The remainder of the tetrapod fossils from the Los Colorados Formation are from its middle and upper parts but have not been stratigraphically organized. The assemblage includes the turtle *Palaeochersis talampayensis* Rougier, De la Fuente and Arcucci, the ornithosuchid *Riojasuchus tenuisceps* Bonaparte the aetosaur *Neoaetosauroides engaeus* Bonaparte, the sphenosuchid *Pseudhesperosuchus jachaleri* Bonaparte, the protosuchid *Hemiprotosuchus leali* Bonaparte, the prosauropod dinosaurs *Riojasaurus incertus* Bonaparte and *Coloradisaurus brevis* Bonaparte, a theropod dinosaur and the tritheledontid cynodont *Chaliminia musteloides* Bonaparte (e.g., Bonaparte, 1970, 1971, 1978, 1980; Lucas and Hunt, 1994; Rougier et al., 1995). The correlative Quebrada del Barro and El Tranquilo formations produce prosauropods (e.g., *Riojasaurus*, '*Mussaurus*') as well (Casamiquela, 1980; Bonaparte and Vince, 1979; Bonaparte and Pumares, 1995). This assemblage clearly is of Late Triassic age and must be post-late Carnian. However, its endemism makes it difficult to correlate precisely. I tentatively consider it an Apachean correlative based on prosauropod abundance, though admittedly this provides a weak basis for correlation.

11.5. Marine cross-correlation

Correlation of the Apachean to the SGCS must be based on indirect lines of evidence. Apachean time is post-Revueltian (~Norian) and pre-Jurassic, so I tentatively correlate it to the Rhaetian (also see Hunt, 1993). However, whether or not it is in part of late Norian age is uncertain. Magnetostratigraphy of the uppermost Chinle Group in eastern New Mexico (Reeve and Helsley, 1972; Molina-Garza et al., 1996), correlated to the Newark Supergroup magnetostratigraphy (Kent et al., 1995), also suggests that the Apachean is latest Triassic ('Norian–Rhaetian').

11.6. Comments

The Apachean is the most difficult Triassic LVF to correlate globally. This almost certainly reflects a provincialization of the global tetrapod fauna. Some of the apparent endemism of Apachean land-vertebrate assemblages may also be due to facies, sampling and taphonomic biases. Rather than recognize a global Apachean LVF, it may be necessary to recognize two or more provincial LVFs during this time interval.

There is no evidence that the Apachean is in part of Jurassic age. The FAD of the crocodylomorph *Protosuchus* appears to correspond closely to the beginning of the Jurassic. *Protosuchus* occurs in the McCoy Brook Formation (Newark Supergroup), the upper Stormberg Group of South Africa and the Dinosaur Canyon Member of the Moenave Formation in Arizona (Colbert and Mook, 1951; Sues et al., 1996). The Moenave record of *Protosuchus* is stratigraphically superposed above Apachean body fossil assemblages of the uppermost Chinle Group (Lucas et al., 1997b).

12. Triassic global tetrapod biochronology

The global tetrapod biochronology proposed here recognizes eight LVFs that encompass Triassic time

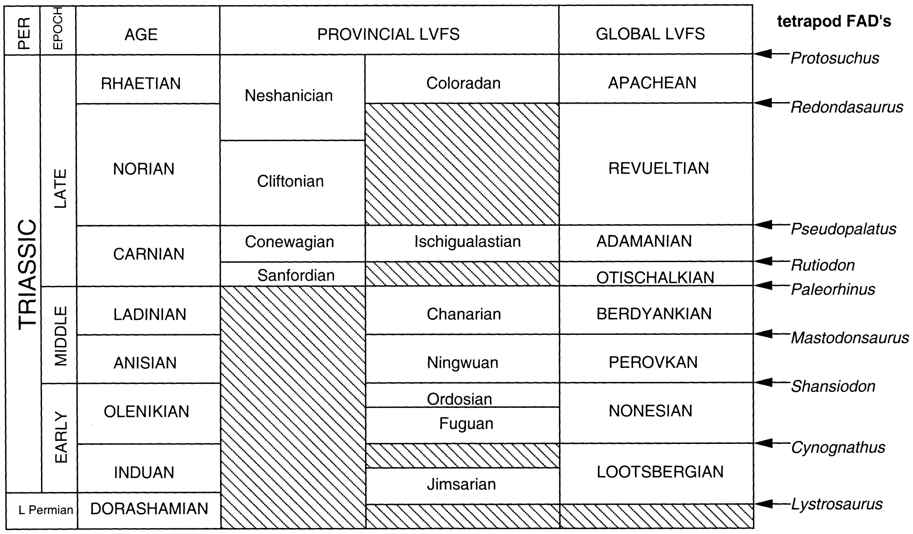


Fig. 14. Triassic provincial and global LVFs, their correlation to the SGCS and the tetrapod FADs that define their boundaries.

(Fig. 14). Most of the boundaries of these LVFs are correlated to stage boundaries of the SGCS, but as the text indicated, these are not always certain correlations.

The eight Triassic LVFs provide temporal resolution as good or better than the seven, internationally recognized Triassic stages of the SGCS. Much as subdivision of some of the marine Triassic stages has been advocated (especially the Induan, Olenikian and Norian), the subdivision of some of the Triassic LVFs needs to be developed (especially the Nonesian and Revueltian). Provincial LVFs provide some basis for such refinement; for example, in China, the Lootsbergian is subdivisible into Jimsarian and Fuguan.

The most problematic stage of the SGCS is the Rhaetian. Ironically, the Apachean is the most problematic LVF. Development of more robust correlations in the Apachean interval is much needed.

Mesozoic biochronology is dominated by the ammonoid paleontologist and marine micropaleontologist. The fossils they study provide the basis upon which most of the Mesozoic SGCS has been built. However, ammonoids and marine microfossils are largely irrelevant to the correlation of the nonmarine strata deposited across the vast expanse of Triassic Pangaea. Tetrapod fossils are key to these correlations, and their organization into the global biochronology presented here is a testable framework for future work.

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