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A REVIEW OF THE REPTILE AND AMPHIBIAN ASSEMBLAGES FROM THE STORMBERG OF SOUTHERN AFRICA, WITH SPECIAL EMPHASIS ON THE FOOTPRINTS AND THE AGE OF THE STORMBERG

by

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ABSTRACT

The Molteno, Elliot, and Clarens formations comprise the continental Stormberg Group of the Karoo Basin of South Africa and Lesotho. The Molteno Formation contains a well preserved macro- and microfloral assemblage but apparently no vertebrates; the Elliot and Clarens formations contain abundant vertebrates but virtually no floral remains. The vertebrate taxa represented by skeletal remains are listed and divided into two assemblages — the lower Stormberg (lower Elliot) and upper Stormberg (upper Elliot and Clarens) assemblages. The abundant, diagnosable footprint taxa are revised and their names reduced to eight genera. These ichnotaxa also fall into two biostratigraphic zones that parallel the skeletal assemblages. Comparison of the faunal assemblages with those of the European type section strongly suggests that the lower Stormberg assemblage is Late Triassic (Carnian-Norian) in age while the upper Stormberg assemblage is Early Jurassic (Hettangian-Pliensbachian) in age. Comparisons with other continental assemblages from other areas suggest that the upper Stormberg (upper Elliot and Clarens formations) assemblage broadly correlates with the upper Newark Supergroup of eastern North America, the Glen Canyon of the southwestern United States, and the lower Lufeng Series of China – all thought to be of Early Jurassic age on the basis of floral and/or radiometric evidence. Based on these correlations, previously published paleobiogeographic maps are revised; these show a shift from Late Triassic floral and faunal provinciality to Early Jurassic homogeneity. This shift was synchronous with a widening of the equatorial arid zone.

CONTENTS

	Page
INTRODUCTION	88
Geological distribution of fossils	88
SKELETAL ASSEMBLAGES	89
Lower Stormberg (lower Elliot) skeletal assemblages	89
Upper Stormberg (upper Elliot and Clarens) skeletal assemblages	90
Comparison of the Stormberg skeletal assemblage with assemblages from other areas	90
Age of Stormberg skeletal assemblages	93
FOOTPRINT ASSEMBLAGES OF THE STORMBERG	94
Lower Stormberg (lower Elliot) footprint assemblage	95
Age-significance of the lower Stormberg footprint assemblage	97
Upper Stormberg (upper Elliot and Clarens) footprint assemblage	99
Age-significance of the upper Stormberg footprint assemblage	101
IMPLICATIONS OF CORRELATION	102
The Triassic	102
The Early Jurassic	104
REFERENCES	105
APPENDIX	109

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INTRODUCTION

Late Triassic and Early Jurassic terrestrial reptile remains from fluvial, lacustrine, and eolian sediments are found on all continents, but the best known diverse assemblages are from the Stormberg Group of southern Africa (fig. 1). These vertebrate-bearing beds are virtually barren of other types of fossils, such as marine invertebrates and megafossil or microfossil plants. As a result, interpretations of the age of these assemblages have been based on comparisons of the vertebrates with those of other areas that preserve continental deposits. The past few years have seen a revision in opinion on the relative ages of terrestrial assemblages from eastern North America, Europe, and China, and this redating directly affects assessments of the age of the Stormberg. Here we: 1) briefly review the Stormberg skeletal assemblages; 2) review and revise the Stormberg footprint assemblages; 3) compare these assemblages to faunules from Europe, North America, South America, and China; and 4) use the redating of all of these early Mesozoic assemblages to arrive at new paleobiogeographic distribution maps for the Triassic and Early Jurassic.

Our review and revision of the footprints is almost completely based on the work of Ellenberger (1970, 1972, 1974). Our review of the skeletal remains is based on the compilations of Haughton (1924), Haughton and Brink (1955), Crompton (1967), Anderson and Anderson (1971), Kermack (1974) Kitching (1977), Anderson and Cruickshank (1978), and Cooper (1981b). It was, of course, Haughton who first gave us a comprehensive look at Stormberg faunules. It is interesting to note that, although new taxa have been discovered and assignments of the age of the assemblages have bounced back and forth between Triassic and Jurassic, the basic Gestalt of the assemblages and the rationale for dating them have not really changed much since Haughton's seminal work of 1924.

Geological distribution of fossils

The Stormberg Group of the Karoo Basin covers large portions of South Africa and Lesotho. Over much of that area it overlies earlier Triassic Beaufort beds or older rocks and underlies the Drakensberg Volcanics of Jurassic and younger age (fig. 2). Three sedimentary formations make up the

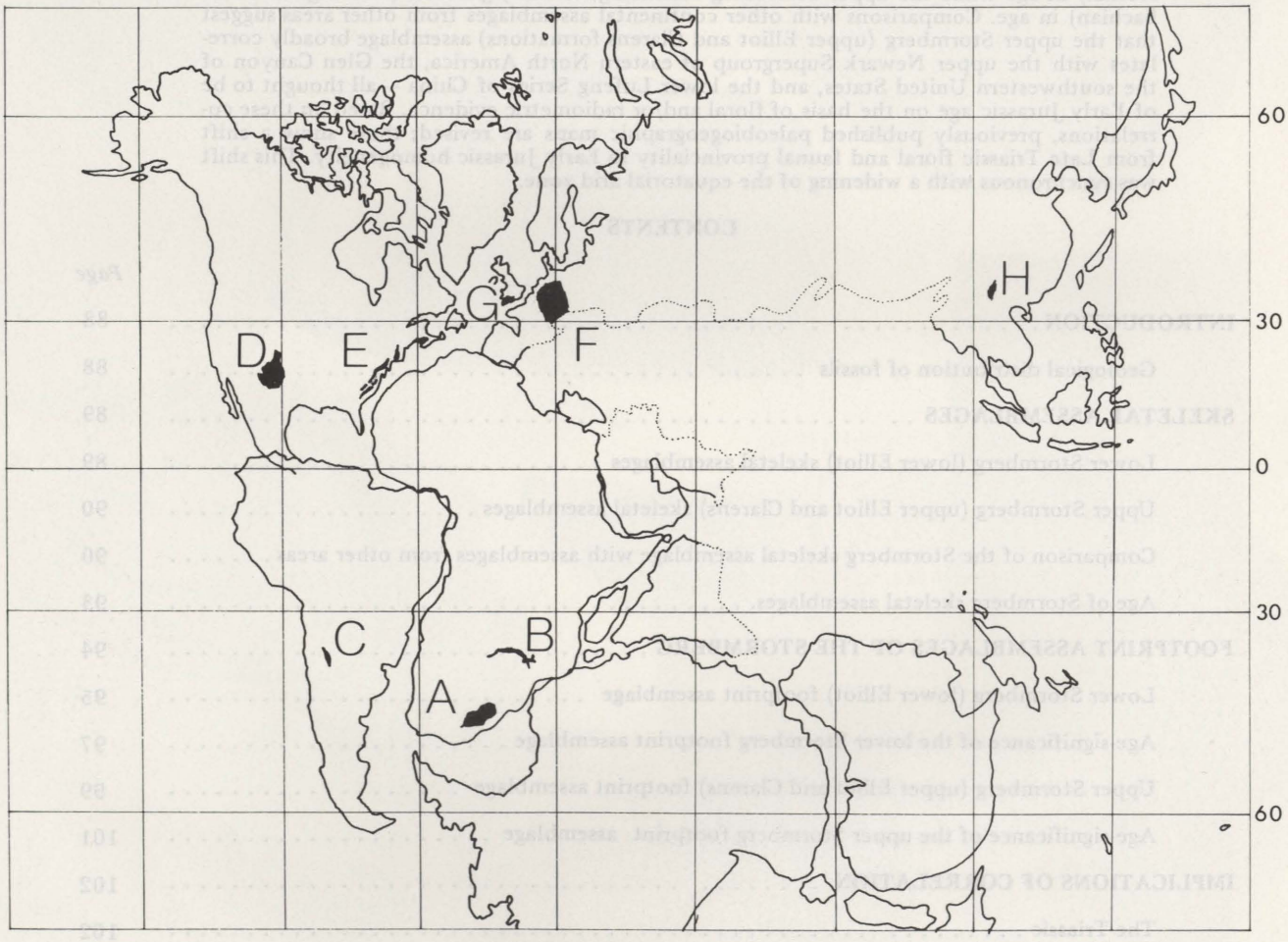

Figure 1

Positions of major areas discussed in text on a map of the positions of the continents during the Early Jurassic (Pliensbachian): A) Karoo Basin, South Africa; B) Middle Zambezi Valley, Zimbabwe; C) Ischigualasto Basin, Argentina; D) Glen Canyon Group, southwestern U.S.A.; E) Newark Supergroup, eastern North America; F) Germanic Basin, Western Europe; G) "Rhaeto-Liassic" fissure fillings, England; and H) Lower Lufeng Series, Yunnan, China. Base map from Smith (1981).

Stormberg Group; these are from oldest to youngest (Kent and Hugo, 1978) the Molteno, the Elliot (formerly called the Red Beds), and the Clarens (formerly called the Cave Sandstone), with the Drakensberg Volcanics on top. These four formations are formally restricted to the Karoo Basin of South Africa and Lesotho (fig. 1), but beds apparently equivalent to these occur in many other areas of southern Africa (Haughton, 1924; Cooper, 1980; Kent and Hugo, 1978).

Recent stratigraphic and sedimentologic studies suggest that parts of the Molteno, Elliot and Clarens formations in the main Karoo Basin are, in part, time-equivalents (Van Heerden, 1977, 1979; Turner, 1971; Le Roux, 1971; Beukes, 1971) (fig. 2). Consequently, parts of the lower Elliot are time transgressive. All the assemblages we refer to as lower Elliot, however, come from the oldest portions of the lower Elliot (according to Van Heerden 1979), and thus comprise the oldest amphibians and reptiles from the Stormberg Group. Because the assemblages from the upper Elliot and Clarens Formations are not separable at the familial level (see Table 1 and below), the lateral time equivalence of the two formations is not so crucial. Here we refer to the Molteno plus the lower Elliot as the lower Stormberg and to the upper Elliot and Clarens formations as the upper Stormberg, following Ellenberger (1970, 1972, 1974).

SKELETAL ASSEMBLAGES

A compilation of skeletal remains from the Stormberg is given in Table 1 and the correlation which results from comparison of these forms with those from other areas is shown in Figure 2. The amphibians and reptiles fall into two distinct assemblages, with the break between them occurring within the Elliot Formation (Ellenberger, 1970; Cooper, 1981b). We base our correlations of skeletal assemblages from the Stormberg on comparisons with assemblages from the Triassic and Jurassic of Europe and comparisons with other vertebrate assemblages from continental rocks for which there is cross-correlation with Europe either using pollen and spores or radiometric dates from sections well dated by marine invertebrates.

Lower Stormberg (Lower Elliot) skeletal assemblage

The basal beds of the Elliot Formation of the Karoo Basin have produced a sparse assemblage of herptiles (Table 1) that allows limited comparisons with other areas. Only the capitosaurid amphibians and plateosaurid prosauropods (*Euskelosaurus* — Van Heerden, 1979) are definitely shared (on a familial level) with the European section and they indicate a no more refined correlation than a Late

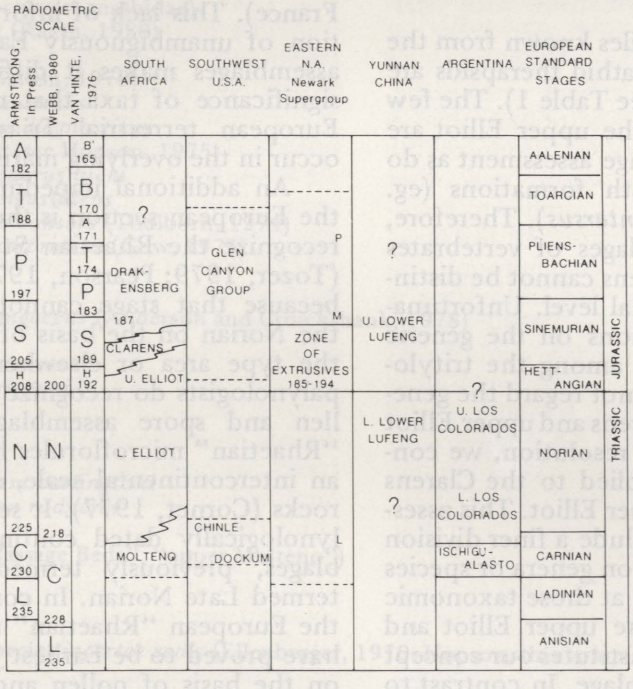

Figure 2

Correlation of the Stormberg Group of South Africa with other areas of continental deposition and the European Standard Stages. In the three columns marked RADIOMETRIC SCALE the letters are abbreviations of stage names as follows: B', Bathonian; B, Bajocian; A, Aalenian; T, Toarcian; P, Pliensbachian; S, Sinemurian; H, Hettangian; N, Norian; C, Carnian; L, Ladinian; A', Anisian. The numbers in the same columns are the radiometrically determined stage boundaries. The numbers in the columns marked SOUTH AFRICA and EASTERN N.A. are radiometric ages for the extrusive rocks in that sequence. The column marked EASTERN N.A. is a composite of all the formations in the different basins of the Newark Supergroup. Abbreviations for formations mentioned in text are as follows: P, Portland Formation of the Hartford Basin, Connecticut and Massachusetts, U.S.A.; M, McCoy Brook Formation of Fundy Group, Nova Scotia, Can.; L, Lockatong Formation of Newark Basin, New Jersey and Pennsylvania, U.S.A.

Triassic age (Hopson, 1980). However, other reptiles found in the lower Elliot and elsewhere have a much more restricted range and are therefore more useful for correlation.

The traversodont cynodont '*Scalenodontoides*' (Crompton and Ellenberger, 1957; Cooper, 1981b) is apparently present in the Wolfville Formation of the Fundy Group of the Newark Supergroup (Nova Scotia, Canada) (Hopson, this volume; Baird and Olsen, In Press). Traversodont cynodonts are unknown above beds confidently dated as Carnian. The Wolfville has produced a diverse although scrappy assemblage of undoubted Late Triassic, probably Carnian age (Carroll, *et al.*, 1972; Baird and Olsen, In Press; Hopson, this volume). There is also a rauisuchid from the lower Elliot (Hopson, pers. comm.) and this group occurs in beds in Europe, North and South America, and China confidently dated as Late Triassic or older. Furthermore, the lower Elliot appears to be in part a red, lateral equivalent of the upper gray beds of the Molteno Formation, the lower part of which has produced plant assemblages of Carnian age (Anderson and Anderson, 1970; Anderson, 1974; Anderson, 1978). We conclude that the skeletal remains support a Late Triassic (Carnian and/or Norian) age for this deposit.

Upper Stormberg (Upper Elliot and Clarens) skeletal assemblage

Of the six families of herptiles known from the Clarens, all but the diarthrognathid therapsids are shared with the upper Elliot (see Table 1). The few families found exclusively in the upper Elliot are very rare and imply the same age assessment as do those families present in both formations (eg. mammals and the theropod *Syntarsus*). Therefore, we conclude that the assemblages of vertebrates from the upper Elliot and Clarens cannot be distinguished objectively on a familial level. Unfortunately, we regard most distinctions on the generic level to be suspect, especially among the tritylodontids and this is why we do not regard the generic differences between the Clarens and upper Elliot as significant. At this level of resolution, we conclude that whatever age is applied to the Clarens must also be applied to the upper Elliot. This assesment does not, of course, preclude a finer division of the upper Stormberg based on genera or species when we have some confidence at those taxonomic levels. The combination of the upper Elliot and Clarens skeletal assemblages constitutes our concept of the upper Stormberg assemblage. In contrast to the lower Stormberg, most of the reptile families from the upper Stormberg are unknown from strata of undoubted Triassic age; rather, most upper Stormberg families are known from undoubted Jurassic deposits (eg. European Jurassic, Morrison Formation) or from beds the age of which is as uncertain as is that of the Stormberg. The division of faunal assemblages corresponds to Cooper's (1981b) *Plateosaurus* Zone (for the lower Elliot) and *Massospondylus* + *Anchisaurus* Zone (for the upper Elliot + Clarens).

The Forest Sandstone of Zimbabwe has yielded the plateosaurid prosauropod *Massospondylus,* the small theropod *Syntarsus,* a protosuchid crocodile, and a small *Glevosaurus*-like sphenodontid rhynchocephalian (Cooper, 1981b; Gow and Raath, 1977, Raath, 1969). This assemblage cannot be distinguished from that of the upper Elliot and Clarens formations, and hence is probably of the same age. To the south of these outcrops in the Limpopo Valley, the Samkoto Formation has produced *Massospondylus* (Cooper, 1981b) and these beds probably correlate with the upper Stormberg and the Forest Sandstone, while the underlying Mpandi Formation has produced *Euskelosaurus (Melanorosaurus)* and thus probably correlates with the lower Elliot (Cooper, 1980).

Comparison of upper Stormberg skeletal assemblage with assemblages from other areas

A principal problem with any attempt to correlate early Mesozoic continental rocks with the European section is that most of the European Early Jurassic section is marine and the few continental beds that are interbedded with marine beds have produced very few terrestrial vertebrates or are themselves of questionable age (eg. the Infralias of France). This lack of information on the composition of unambiguously Early Jurassic continental assemblages makes it difficult to assess the age-significance of taxa that range to the top of the European terrestrial Triassic but which do not occur in the overlying marine Early Jurassic.

An additional impediment to correlation with the European section is the recent tendency not to recognize the Rhaetian Stage of the Late Triassic (Tozer, 1979; Pearson, 1970; Hallam, 1981, 1982) because that stage cannot be distinguished from the Norian on the basis of marine invertebrates in the type area or elsewhere. On the other hand, palynologists do recognize a distinct "Rhaetic" pollen and spore assemblage (Schuurman, 1979); "Rhaetian" microflorules have been recognized on an intercontinental scale, especially in continental rocks (Cornet, 1977). It seems likely that most palynologically dated continental vertebrate assemblages, previously termed Rhaetian, should be termed Late Norian. In contrast, however, most of the European "Rhaetian" megafossil plant florules have proved to be Earliest Jurassic (Achilles, 1981) on the basis of pollen and spores. On top of this confusion, the status of European "Rhaeto-Liassic" bone-bed assemblages and "Rhaetic" continental vertebrate assemblages is very uncertain; some may be Norian, others Jurassic (Clemens, 1980). Thus, the German Stubensandstein and Knollenmergel provide the only secure comparative base for the European Norian and hence the latest Late Triassic. We therefore follow Tozer (1979) and Pearson (1970) and recognize the Norian as the youngest

Table 1

LIST OF THE STORMBERG TETRAPOD TAXA KNOWN FROM SKELETAL REMAINS: CLASS, ORDER, FAMILY, GENUS AND SPECIES ARE GIVEN. SOURCE IS ANDERSON AND ANDERSON (1970), EXCEPT AS NOTED.

UPPER STORMBERG
Clarens Formation
Reptilia
Crocodiliomorpha
Protosuchidae (Stegomosuchidae)
Notochampsa istedana
Pedeticosauridae (Sphenosuchidae)
Pedeticosaurus leviseuri
Saurischia
Anchisauridae (includes Plateosauridae)
Massospondylus carinatus (see Cooper,1981)
Ornithischia
Heterodontosauridae
Geranosaurus atavus
Therapsida
Tritylodontidae
Tritylodontoideus maximus
Diarthrognathidae
Diarthrognathus broomi
Upper Elliot Formation
Reptilia
Chelonia
?Proganochelyidae (Kitching, pers. comm., 1980)
Crocodiliomorpha
Protosuchidae (Stegomosuchidae)
Erythrochampsa longipes
Orthosuchus stormbergi
Pedeticosauridae
Sphenosuchus acutus
Saurischia
Anchisauridae (includes Plateosauridae) (see Galton and Cluver, 1976)
Massospondylus carinatus (see Cooper, 1981a)
Podokesauridae (Procompsognathidae)
Syntarsus sp. (Raath, 1980)
Ornithischia
Fabrosauridae (see Galton, 1978)
Fabrosaurus australis
Lesothosaurus diagnosticus
Heterodontosauridae (see Hopson, 1975)
Heterodontosaurus tucki
Lycorhinus angustidens
Abrictosaurus consors (Thulborn, 1974)
Lanasaurus scalpridens (Gow, 1975)
Therapsida
Tritylodontidae
Tritylodon longaevus (Anderson and Cruickshank, 1978)
Tritheledontidae
Pachygenelus monus
Trithelodon riconoi
Mammalia
Docodonta
Morganucodontidae
Erythrotherium parringtoni
Megazostrodon rudnerae
LOWER STORMBERG
Lower Elliot Formation (= "Passage Beds", "upper Molteno")
Amphibia
Temnospondyli
Capitosauridae
Genus and Species *incertae sedis* (Ellenberger, 1970; Hopson, this volume)
Reptilia
Thecodontia
Rauisuchidae (Prestosuchidae)
Genus and Species *incertae sedis* (Hopson, this volume); also Seeley, 1894, fig. 1 for large maxilla that was incorrectly referred to prosauropod *Euskelosaurus* – Galton, in prep.)
Saurischia
Anchisauridae (includes Plateosauridae and Plateosauravidae)
Euskelosaurus browni
Melanorosauridae
Melanorosaurus readi (Haughton 1924) (regarded as valid taxon following Van Heerden, 1977, and Cooper, 1980 not junior synonym of *Euskelosaurus* as stated by Van Heerden, 1979 – Galton, in prep.)
?New Genus and Species (Van Heerden, In Press)
Therapsida
Traversodontidae
Scalenodontoides macrodontes (Hopson, this volume)

stage of the Triassic.

The dinosaurian families Anchisauridae (including Plateosauridae, Galton, 1971) and Procompsognathidae (i.e. small theropods = coelurosaurs), and possibly the turtle family Proganochelyidae (Kitching, pers. comm.) occur in the upper Stormberg and in the Norian of Germany, but no genera are shared. A newly discovered faunule from continental rocks in the northeastern France shares morganucodontid mammals with the upper Stormberg assemblage, but the age of this faunule has not been determined with confidence (Sigogneau-Russell, 1978; Clemens, 1980). The "Rhaeto-Liassic" bone beds of Europe lie between fully marine Early Jurassic rocks and continental Late Triassic rocks. Their exact correlation with the European standard stages is not precisely known, but they could be as old as Norian or Hettangian, and all the occurrences need not be of the same age (Clemens, 1980). The families Tritylodontidae and Morganucodontidae occur in the upper Stormberg and in at least some of the "Rhaeto-Liassic" bone beds; the genus *Tritylodon* is originally from the "Rhaeto-Liassic" bonebeds at Wurttemberg (Lydekker, 1887); Clemens, 1980) and also occurs in the upper Stormberg (upper Elliot) (Clemens *et al.*, 1979).

Fortunately, there are early Mesozoic terrestrial vertebrates preserved in fissure fillings in Great Britain associated with marine fossils and/or floral remains that permit direct correlation with nearby marine rocks of unquestioned age. Some of these small pockets share a large proportion of their taxa with the upper Stormberg assemblage. Robinson (1957) divided the fissure assemblages into two age groups. The older set produces the peculiar gliding reptile *Kuehneosaurus* and other lepidosaurs. *Kuehneosaurus* is very similar to *Icarosaurus* from the Lockatong Formation of the Newark Basin portion of the Newark Supergroup (Colbert, 1966, 1970). The age of the Lockatong is Late Carnian (Cornet, 1977; Olsen, 1980a) and on that basis the older set of fissure fills could be of the same age. The younger set of fissure fillings contains mammal (kuehneotheriid, haramiyid, and morganucodontid), tritylodontid, and lepidosaur material as well as abundant floral remains belonging to the *Himeriella* (= *Cheirolepis*) association. Pacey (1978, cited in Kermack, Mussett, and Rigney, 1981) has restudied this association and concluded that it is Early Jurassic (probably early Sinemurian) in age. Morganucodontids, and tritylodontids (Kermack, 1956) occur in both the Jurassic fissure fillings and the upper Stormberg assemblage.

At this writing, it is important to stress that there are no records of morganucodontid mammals or tritylodontids in unambiguously Late Triassic rocks. In fact, many morganucodontid and tritylodontid remains from Europe come from rocks of undoubted Jurassic age (such as the Middle Jurassic – Freeman, 1976a, 1976b; Charlesworth, 1838; Simpson, 1928) or are correlated with the Jurassic on the basis of marine (*Oligokyphus* : Kuhne, 1956) or floral evidence (*Morganucodon* : Kermack, Musset, Rigney, 1981).

Other deposits that have produced skeletal taxa shared with the upper Stormberg assemblage and have yielded independent age-correlative data include the Newark Supergroup of eastern North America (Olsen and Galton, 1977), the Glen Canyon Group of the southwestern United States, and the Lower Lufeng Series of China. The younger beds of the Newark Supergroup share a series of taxa with the upper Stormberg assemblage. On a familial level, the Portland Formation of the Hartford Basin of Connecticut and Massachusetts shares protosuchian crocodiles and anchisaurid prosauropods. These remains are associated with palynoflorules ranging in age from Pliensbachian to Toarcian (Cornet, 1977; Olsen, 1980a). K/Ar dates from the basalt flows underlying the Portland Formation range from 194–185 Ma (Masterton, 1979), indicating an Early Jurassic age for the basalts (Olsen, McCoy and Thomson, 1982) and overlying beds. The McCoy Brook Formation of the Fundy Basin of Novia Scotia, Canada is interbedded with and overlies the North Mountain Basalt of Early Jurassic age (Olsen, 1981). Skeletal remains from the McCoy Brook Formation include an anchisaurid prosauropod dinosaur (cf. *Ammosaurus*), a small fabrosaurid dinosaur, a ?procompsognathid dinosaur (aff. *Syntarsus*), and a protosuchid crocodile (Olsen and Baird, 1982 and In Prep.). These beds almost certainly correlate with the upper Stormberg. In addition, this latter assemblage is especially similar to that from the Forest Sandstone of Zimbabwe. All the taxa (on at least the familial level) present in the Forest Sandstone are also found in the McCoy Brook. In addition, the sphenodontid present in the Forest Sandstone is generically (and possibly specifically) indistinguishable from the sphenodontid from the McCoy Brook Formation. Both forms are similar, but not identical, to *Glevosaurus* from the fissure fills of Great Britain (Robinson, 1957, 1973; Pacey, 1978). The resemblance of the Jurassic part of the Newark to the upper Stormberg is especially obvious when their footprint assemblages are compared (see below).

The Glen Canyon Group of the southwestern United States (Wingate, Moenave, Kayenta, and Navajo formations) shares a growing list of skeletal forms with the upper Stormberg assemblage on a familial level and shares a number of genera as well. On a familial level, the Glen Canyon shares tritylodontids (Lewis, 1958; Kermack, 1982), fabrosaurid ornithischian dinosaurs (Colbert, 1981), heterodontosaurid ornithischian dinosaurs (Crompton, pers. comm.), prosauropod dinosaurs (Galton, 1976), and protosuchian crocodiles (Smith and Crompton, 1980) with the upper Stormberg. On a generic level, the upper Stormberg and the Glen Canyon share the prosauropod *Massospondylus* (Crompton, pers. comm.). The upper Newark Supergroup and the Glen Canyon Group share on a familial level sphenodontid rhynchocephalians, protosuchid crocodiles, plateosaurid prosauropod dinosaurs, fabrosaurid dinosaurs, and procompsognathid theropod dinosaurs (Olsen, 1980a; Olsen and Baird, In Press) and they share on a generic level the prosauropod *Ammosaurus* (Galton, 1976). It should also

be noted that the skull of *Ammosaurus* Marsh 1889 is very inadequately known (Galton, 1976) and the skull of the American species of *Massospondylus* Owen 1854 lacks any postcranial skeleton. Consequently, it is possible, but by no means certain, that all the material described as *Ammosaurus major* (Marsh) should be referred to *Massospondylus*. The Glen Canyon Group has produced a pollen and spore assemblage from near its base (Moenave Formation) of Early Jurassic age (Sineumurian or Pliensbachian) (Cornet quoted in Olsen and Galton, 1977). In addition, the Glen Canyon Group shares the tritylodontid *Oligokyphus*, kuehneotheriid and haramiyid mammals, and ?protosuchid crocodiles with the English Jurassic fissure fills (Crompton, Jenkins, and Sues, pers. comm.). A tritylodontid recently described from the Glen Canyon Group, *Kayentatherium* Kermack 1982, is related to *Tritylodon* from the Stormberg. The presence of a *Tritylodon*-like tritylodontid in the Kayenta Formation of the Glen Canyon Group has been known for two decades and has been used as evidence by Lewis, Irwin, and Wilson (1961) to conclude that the age of the Glen Canyon Group is Late Triassic because the Stormberg was considered "typical" Late Triassic. Kermack (1982) argues, however, that while at least one Glen Canyon tritylodontid (*Kayentatherium*) is related to *Tritylodon*, it actually suggests an Early to Middle Jurassic age for at least the Kayenta Formation of the Glen Canyon Group (Kermack, 1982).

The Lower Lufeng Series of China produces vertebrates very similar to those of the Upper Stormberg. On a familial level, morganucodontid mammals, tritylodontids, plateosaurid prosauropod dinosaurs, fabrosaurid and heterodontosaurid ornithischian dinosaurs (Young, 1982), protosuchian crocodiles, and sphenosuchid crocodiliomorphs are shared with the upper Stormberg assemblage (Young, 1951, 1982; Simmons, 1965). On a generic level, the Lufeng shares *Morganucodon* with the English fissure fills (Clemens, 1979). Floral evidence strongly suggests that the lower Lufeng, too, is Early Jurassic in age (Cui, 1976; Sigogneau-Russell and Sun, 1981).

The only other deposit producing a skeletal assemblage resembling that of the upper Stormberg is the Los Colorados Formation of Argentina. It shares plateosaurid prosauropod dinosaurs, protosuchid crocodiles, sphenosuchid crocodiliomorphs, and tritylodontids on a familial level with the upper Stormberg (Bonaparte, 1971, 1978, 1980, 1981a,b), and in addition the skull of the plateosaurid *Coloradia brevis* Bonaparte (1981b) is very similar to that of *Massospondylus*. It also shares stagonolepid, rauisuchid, and ornithosuchid thecodonts and plateosaurid prosauropods on the familial level with undoubted Late Triassic beds (Bonaparte, 1978), but the material described as *Plateosaurus* sp. by Casamiquela (1980) is referable to *Coloradia*. Finally the Los Colorados shares "melanorosaurid" (sensu Van Heerden, 1979, In Press) and plateosaurid prosauropods (*Euskelosaurus* from the Elliot [Van Heerden, 1979]), and rauisuchid thecodonts with the lower Elliot. Unfortunately, no other forms of age-correlative data have been discovered in the Los Colorados so the assemblage is of no real help in dating the Stormberg.

The incompleteness of terrestrial vertebrate assemblages from the early Mesozoic of Europe tends to force us to correlate assemblages from other areas with either the Carno-Norian (which is fairly well known in Europe) or the Early Jurassic (which is so very poorly known in Europe). The upper Los Colorados assemblage could, in fact be transitional between "typical" Late Triassic assemblages, such as that from the Chinle Formation of the southwestern United States, and what are thought to be Early Jurassic assemblages on the basis of independent data, such as the upper Newark Supergroup. Without pollen and spores, megafossil plants, marine invertebrates, or radiometric dates, it is impossible to decide whether the Los Colorados assemblage is: 1) of latest Triassic age and the oldest to have several reptile groups otherwise "typical" of the Early Jurassic; 2) of Early Jurassic age, with the last of the rauisuchid, ornithosuchid, and stagonolepid thecodonts surviving; 3) of intermediate age between other known assemblages; or 4) of late Triassic age and indicating that all the other Early Jurassic assemblages discussed above are really Triassic. Our opinion, based on the preponderance of vertebrates "typical" of well dated Triassic deposits elsewhere, is that the Los Colorados is latest Norian (latest Triassic) in age and does contain a true transitional faunule.

However, more precise stratigraphical information is needed to ensure that this transitional nature is not the result of mixing finds from different levels because Bonaparte (1978:220) notes that the fauna comes from the top 300m.

Age of the Stormberg skeletal assemblage

On the basis of direct correlation with the European section using taxa based on skeletal remains, the upper Stormberg appears to be no older than very latest Triassic and the bulk of the evidence suggests an Early Jurassic age. This conclusion agrees with that of Kermack (1974), Olsen and Galton (1977), and Cooper (1981b). The Early Jurassic age of the upper Stormberg is also supported by skeletal evidence from other deposits correlated with the European section by floral means. Finally, the Jurassic age of the upper Stormberg is completely consistent with radiometric dates from the interfingering and overlying lower Drakensberg volcanics which cluster around 187 Ma (Fitch and Miller, 1971).

In summary, we agree with Colbert's (1981, p. 56) comment that, "To place this horizon [the Kayenta Formation] within the Jurassic, it will be necessary to reassign to the Jurassic such formations as the Red Beds and Cave Sandstone in South Africa and the Lufeng Formation in China . . .".

FOOTPRINT ASSEMBLAGES OF THE STORMBERG

The reptilian footprints from the Stormberg re-

mained essentially unstudied until the publication of Ellenberger's works. In his most extensive contributions, Ellenberger (1970, 1972, 1974) described some 174 new species and 69 new genera of footprints. While we have not had the opportunity to examine the material first-hand, Ellenberger's figures are explicit and, as we will show below, are directly comparable to material from elsewhere. We also feel that Ellenberger's differentiation of the track-bearing horizons of the Stormberg Group into two broad faunal zones reflects a real faunal change through time that is equivalent to the break seen in skeletal remains, and equivalent to the faunal transition seen at the end of the Triassic elsewhere.

A comparison of figures of Stormberg footprints known from the Newark Supergroup of eastern North America (Olsen, 1980a, 1980b) reveals a profound similarity between the upper Stormberg assemblage (Zone B of Ellenberger, 1970) and that of the upper Newark (Zone 3 of Olsen and Galton, 1977). Earlier published works on Newark footprints (eg. Hitchcock, 1848; Deane, 1861; Lull, 1915, 1953) are badly in need of taxonomic, morphologic, and stratigraphic revision; close resemblance between the Newark and Stormberg footprint assemblages has only become apparent as new material has been found and the older material revised. After careful comparison of Ellenberger's figures with material at our disposal, we conclude that most of the forms described from the Stormberg are either congeneric with Newark forms or are indeterminate (figs. 3–5; the valid Stormberg taxa and their synonymies are listed in the Appendix). Of the 24 genera described from the lower Stormberg assemblage (lower Elliot, zone A) by Ellenberger (1972), 15 appear to us to be founded on indeterminate material, seven are congeneric with European forms also found in the Newark (fig. 3), and one very similar to a form found in the Glen Canyon Group of the southwestern United States might be valid. This leaves *Pentasauropus* as the only definitely valid endemic genus (fig. 3) in the lower Stormberg. Of the 46 genera founded on upper Elliot and Clarens material (Zone B of Ellenberger, 1970), 26 appear to be based on indeterminate material, 19 are congeneric with Newark forms, and one (*Episcopopus*) is distinct but possibly indeterminate. Ellenberger *et al.* (1967) and Ellenberger (1970) have already made comparisons of Stormberg tracks with tracks from the European early Mesozoic and we agree with the essentials of their correlations. Unfortunately, neither the diversity nor the quality of the European Late Triassic and Early Jurassic tracks compares with those from either the Newark or the Stormberg.

The criteria on which we base our assessments of the Stormberg tracks are four; these are listed below along with an explanation of each:

I. *Tracks are distinct from Trackmakers*

The first criterion reflects the dichotomy between the trackmaker and its artifact, the track. It is based on Baird's (1957) maxim that "a footprint is not the natural mold of a morphological structure but is, instead, the record of that structure in dynamic contact with a plastic substrate." The trackmaker had an existence as an organism belonging to a population with properties we would use to define species of higher categories. The track is a shadow of the form of the organism, viewed in the dim light of behaviour, substrate nature, and diagenesis. The track never had most of the properties of an organism. Without the body-fossil dead in its tracks we can at best imagine the Platonic ideal of which the tracks are shadows – i.e., the foot. Tracks are best grouped objectively, therefore, by their shape.

The dichotomy between the track and trackmaker is reflected by the fact that, although we use a Linnean-style system for the tracks, the system is separate from that used for organisms; the meaning of taxonomic categories at lower levels is very different in ichnology and osteological zoology. This is reflected by the exclusion of ichnofossils from consideration by the International Commission on Zoological Nomenclature (ICZN, 1964). We refer to the components of the binomen as the ichnogenus and ichnospecies to differentiate them from biological taxa; ichnogenera and ichnospecies probably do not correspond to zoological genera and species, respectively (Baird, 1980). In most cases an ichnogenus probably corresponds to the primitive state for foot structure in an entire group. For example, the ichnogenus *Grallator* could have been made by any of the conservative members of the suborder Theropoda from any part of the Mesozoic.

The ichnogenus *Anomoepus* could have been made by cursorial members of the families Fabrosauridae, Hypsilophodontidae, some Iguanodontidae, Psittacosauridae, and some Leptoceratopsidae. Nonetheless the stratigraphic distribution of footprint taxa reflects the distribution of some taxonomic categories of organisms (although we may not know what categories they are) and in that way serve as a parallel biostratigraphic system such as Ellenberger has produced for the Stormberg and upon which we are elaborating.

II. *Determinate tracks show Trackmaker morphology.*

Our second criterion follows from the first and reflects the unfortunate fact that most footprints are very poor records of foot structure. Those that reveal little of trackmaker's morphology should not, in our view, be formally named. Operationally, the recognition of tracks that deserve names rests on the presence of pads or some unique feature, such as the five short subequal toes of *Pentasauropus* (fig. 3). We have judged many of Ellenberger's ichnotaxa indeterminate because the tracks show too little structure of the trackmaker and too much of the condition of the substrate or of the animal's movement. This is despite the tautology – used all too often as a justification for naming bad

tracks – that any individual track can be differentiated from all others by its unique shape. However, this uniqueness has no taxonomic significance if it does not relate to the structure of the organism that produced it.

III. *Most useful aspects of track morphology reflect osteology.*

Our third criterion is based on the suggestion by Baird (1957) that the most useful attributes of a track are those that reflect osteological characters of the trackmaker's foot. These features are most likely to allow placement of tracks in categories that parallel (but may not be identical to) osteological taxa; they are hence most likely to allow the recognition of ichnotaxa that are useful as: 1) biostratigraphic indicators; and 2) clues to animals that lived in an area but left no bones.

IV. *Footprints in the same "growth series" should be synonymized.*

Our fourth criterion follows from the first and third by recognizing that vertebrates grow and that the bones of the feet commonly change in shape as their size changes. Shape differences that reflect osteological differences are those which are most useful for our purposes. But one category of shape differences is not valid for dividing tracks or bones into lower categories: namely those characters that vary continuously with size and that are attributable to, or at least not differentiable from, allometric growth. It makes sense to group all the footprints fitting such a "growth series" in the same taxonomic category when the apparently systematic differences in shape cannot be distinguished from those due to changes in size during the ontogeny of individuals of the same species However, some size ranges of a particular ichnotaxon may be restricted stratigraphically and therefore we occasionally use an ichnosubgenus designation to retain the utility of a footprint name (see *Grallator,* below).

Below, we describe and redefine the valid footprint taxa from the Stormberg by applying the above criteria to the drawings and photographs given by Ellenberger (1972, 1974). These taxa are listed with their synonymies in the Appendix.

Lower Stormberg (lower Elliot) footprint assemblage

Ichnofamily Chirotheriidae Abel 1935

Ichnogenus *Brachychirotherium* Beurlen 1950

Brachychirotherium spp.

Discussion:

The most abundant recognizable tracks from the lower Stormberg appear to be members of the ichnogenus *Brachychirotherium* Beurlen 1950 (Haubold, 1971) (Brachychirotherian group of Baird, 1957) (fig. 3). *Brachychirotherium* is characterized by a five-toed pes impression in which digit V is reduced to an oval pad posterolateral to digit IV. From longest to shortest, the digits of the pes are III, IV, II, I, V. The five-toed manus points more or less anteriorly and has digits of subequal length. The relatively primitive structure of the pes and manus suggest that *Brachychirotherium* was produced by a large thecodont, perhaps a rauisuchid (Padian and Olsen, In Prep).

Given this assignment it is difficult to imagine how advanced bipedal thecodont (rauisuchids or stagonolepids with a reduced digit V) tracks could be distinguished from the tracks of other archosaurs with relatively primitive feet such as prosauropods or crocodiliomorphs. Most thecodonts, prosauropods, and crocodiliomorphs have the same phalangeal formula and relative pedal proportions. The ankles differ, but these differences would probably not have shown up in the tracks. On this basis, we conclude that bipedal *Brachychirotherium*-like tracks cannot be assigned definitely to either thecodonts or prosauropods or crocodiliomorphs. Further, definite assignment of bipedal *Brachychirotherium*-like tracks to the ichnogenera *Brachychirotherium, Navahopus,* or *Otozoum* cannot be accomplished without some external considerations that lessen the independence of the track information. The diagnostic criteria of these ichnotaxa pertain to the manus, not the pes. In track assemblages in which *Brachychirotherium* tracks are definitely present, we prefer to group bipedal *Brachychirotherium*-like footprints in *?Brachychirotherium* sp., with full knowledge that were manus impressions present in some of these, we might group the tracks in some other ichnogenus. We thus group uncertain tracks with the more "primitive" ichnotaxa present in the same assemblage and we consider this the conservative practice.

Ichnofamily Navahopodidae *nov.*

Ichnogenus *Tetrasauropus* Ellenberger 1970

Tetrasauropus unguiferus Ellenberger 1970

Discussion:

One manus and pes set figured by Ellenberger (1972) closely approximates the ichnogenus *Navahopus* recently described from the Glen Canyon Group of the Southwestern United States by Baird (1980) (fig. 3). Like *Navahopus, Tetrasauropus* is characterized by a *Brachychirotherium*-like pes in which there is no impression (or only a slight impression) of the pad beneath digit V, and a manus with an impression of a very large, falciform, medially directed claw on digit I; the other digits of the manus are much smaller with some lateral di-

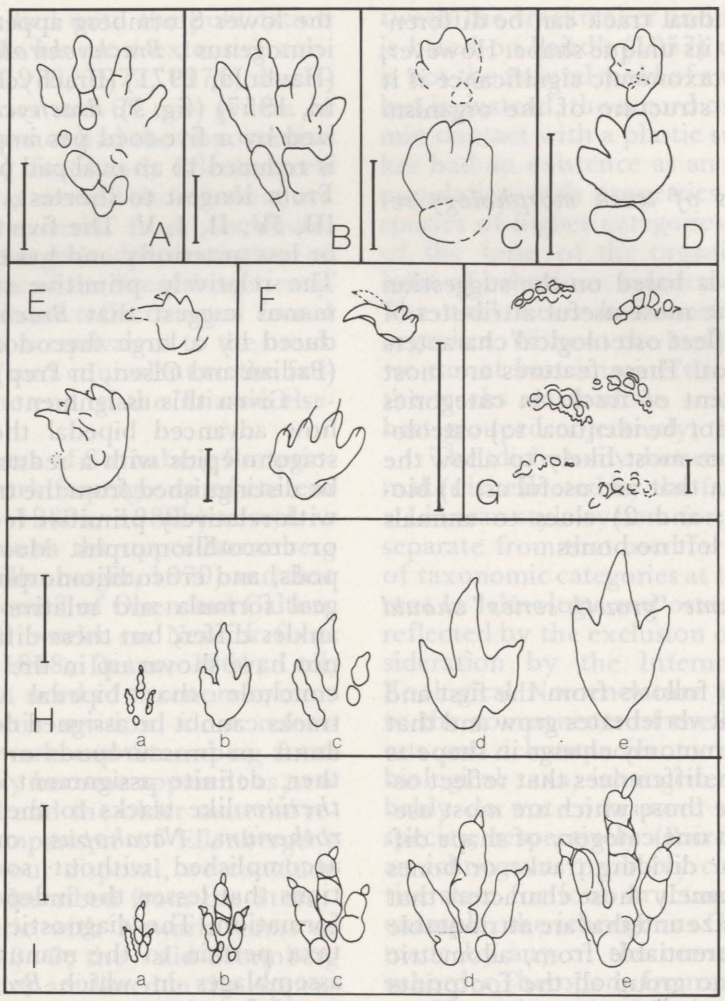

Figure 3

Footprints of the lower Stormberg assemblage compared with forms from the Newark Supergroup, Glen Canyon Group, and Europe. All tracks are drawn as left pes or manus impressions. Stormberg taxa (A,C,E,G,H) are traced and simplified from Ellenberger (1970). Scale 20 cm.:

A) bipedal *Brachychirotherium* sp. (*Pseudotetrasauropus bipedoida* of Ellenberger, 1970, pl. II, fig. 28).

B) bipedal *Brachychirotherium* sp. from the Pekin Formation (Middle Carnian) of the Newark Supergroup (North Carolina, U.S.A., Sanford Basin) (specimen not collected).

C) quadrupedal *Brachychirotherium* sp. (*Deuterosauropodopus minor* (type A) of Ellenberger, 1970, pl. IV, fig. 51A)).

D) *Brachychirotherium thuringiacum* from Middle Keuper (Norian) of Germany (traced from Freyberg, 1965).

E) *Tetrasauropus unguiferus* (traced from Ellenberger, 1970, pl. III, fig. 36).

F) *Navahopus falcipollex* (traced from Baird, 1980, fig. 12.3, from the Navajo Sandstone (E. Jurassic) of the Glen Canyon Group, Arizona, U.S.A.

G) *Pentasauropus incredibilis* (traced from Ellenberger, 1970, pl. IV, fig. 51A).

H) *Grallator* spp. from the lower Stormberg assemblage: a) *Prototrisauropus graciosus* of Ellenberger, 1970, pl. I, fig. 14; b) *Qemetrisauropus minor* of Ellenberger, 1970, pl. I, fig. 7; c) *Prototrisauropus rectilineus v. lentus* of Ellenberger, 1970, pl. II, fig. 19; d) *Qemetrisauropus princeps* of Ellenberger, 1970, pl. I, fig. 6; e) *Prototrisauropus crassidigitus* of Ellenberger, 1970, pl. I, fig. 16).

I) *Grallator* spp. from the Early Jurassic portion of the Newark Supergroup (apparently identical forms occur in the Late Triassic (Norian) portion of the Newark as well): a) *Grallator* sp. from the Towaco Formation of Newark Basin (Hettangian) (redrawn from Olsen 1980b, fig. 20, Ab); b) *Grallator* sp. from Towaco Formation (redrawn from Olsen, 1980b, fig. 20, Ad); c) type of *Eubrontes platypus* of Lull 1904, original, A.C. 15/4, from Turners Falls Sandstone (Hettangian), Deerfield Basin, Massachusetts, U.S.A.; d) type of *Eubrontes divaricatus* of Hitchcock 1865, original, A.C. 58/1,(E. Jurassic)of Connecticut Valley, Connecticut or Massachusetts, U.S.A.; e) *Grallator* sp. from Towaco Formation (Hettangian) of Newark Basin, New Jersey, U.S.A. (redrawn from Olsen, 1980b, fig. 20, A, f).

gits often not impressing. *Navahopus* might belong in the ichnogenus *Tetrasauropus,* the latter name having priority; however, we do not formally suggest synonymy because, as Baird (1980, p. 228) notes, " . . . better material would be required for any definitive comparison." It is possible that *Tetrasauropus* is a distorted example of *Brachychirotherium.* Baird (1980) suggests that the falciform claw on the manus and the primtive (for saurischians) structure of the foot indicate that both *Navahopus* and *Tetrasauropus* could have been produced by prosauropod dinosaurs, whose bones are found in both deposits.

Ichnofamily Grallatoridae Lull, 1953

Ichnogenus *Grallator* Hitchcock 1858

Grallator spp.

Discussion:

Three-toed footprints referable to the ichnogenus *Grallator* are the second most abundant type of track in the lower Stormberg assemblage (fig. 4, Table 2). *Grallator,* as currently defined (Baird, 1953; Lapparent and Motenat, 1967; Olsen, 1980b), has digits II, III and IV always impressing with digit III always the longest, and digits IV and II subequal in length. Occasionally, the tip of the claw on digit I impresses. Except for a single possible resting example from the Newark Supergroup, there is never a manus impression.

The ichnogenera *Grallator, Anchisauripus,* and *Eubrontes* as illusted by Lull (1953) and by the type specimens, show differences in proportions that probably reflect real differences in the osteology of the feet of the trackmakers (Olsen, 1980b; Baird, 1953) and the main factor responsible for these differences appears to be the relative length of digit III. Olsen (1980b) has shown that the relative length of digit III changes continuously with the size of tracks traditionally referred to these three ichnogenera, and suggested that this change in shape with size forms a continuum similar to what would be expected in an ontogenetic series of a single ichnotaxon. It is therefore reasonable to synonymize the names *Eubrontes* Hitchcock 1845 (the type (A.C. 45/8) being indeterminate) and *Anchisauripus* Lull 1904 with *Grallator* Hitchcock 1858, because specimens within this series cannot be objectively distinguished on a generic level. We suggest using subichnogenus designations to denote tracks in the three broad size categories as represented by the three original generic names. For example, large tracks fitting the same allometric curve as *Grallator* (only larger) are more usefully termed *Grallator (Eubrontes)* sp. than *Grallator* sp. alone. Thus, although *Grallator* spp. are distributed through the entire Newark Supergroup of eastern North American, *Grallator (Eubrontes)* spp. appear only in the latest Triassic and become abundant only in the Jurassic (Olsen, 1980a). Only *Grallator (Grallator)* spp. are present in the lower Stormberg assemblage.

As noted by Heilmann (1927), Lull (1904), Schmidt (1959), Peabody (1948), and Baird (1953), tracks traditionally referred to *Grallator* were almost certainly made by small theropod dinosaurs and according to Lull (1953) *Eubrontes* was produced by large theropod dinosaurs. On the other hand, despite the obvious structural intermediacy between *Grallator* and *Eubrontes, Anchisauripus* tracks were interpreted by Lull (1904) as having been produced by prosauropod dinosaurs, such as *Anchisauripus* and *Ammosaurus* from the Connecticut Valley (hence Lull's epithet *Anchisauripus*). Recently, Baird (1980) has convincingly demonstrated that prosauropods could never have produced *Anchisauripus*-like tracks but that these tracks were also made by theropods (coelurosaurs or carnosaurs). The structural continuity among *Grallator, Anchisauripus,* and *Eubrontes* suggests to us that *Grallator sensu lato* could have been made by various taxa of adult theropods of various sizes or by juveniles of one or more larger theropod taxa. This mirrors Ostrom's (1969) observations on the structural continuity between what are usually called coelurosaurs and carnosaurs. However, the fact that we recognize only one ichnogenus, *Grallator,* does not imply that we think these tracks were made by only one dinosaur species, genus, or even family of reptiles.

Ichnofamily Pentasauropodidae nov.

Ichnogenus *Pentasauropus* Ellenberger 1970

Pentasauropus maphutsengi Ellenberger 1970

Discussion:

Pentasauropus (fig. 3g) is characterized by its large size, very short stride, and subequal manus and pes impressions that are similarly shaped, with manus and pes bearing five subequal toes. No named early Mesozoic tracks approach the configuration of *Pentasauropus* and despite the fact the tracks themselves are poor, they are unmistakable and represent a valid ichnogenus. Tracks that may be referable to *Pentasauropus* are found in the Gettysburg Shale of the Gettysburg Basin of the Newark Supergroup (Baird, 1957, pers. comm.).

These tracks from the Gettysburg Shale are found in association with *Brachychirotherium* spp. (Baird, pers comm.). The only early Mesozoic reptile group with feet both large enough and with toes short enough to have made *Pentasauropus*-type tracks is the dicynodontid mammal-like reptiles.

Age-significance of the Lower Stormberg footprint assemblage

The generally poor quality of the lower Stormberg footprint assemblage decreases its age-significance, and therefore only limited comparisons are possible with tracks from elsewhere. However, on a

broadly defined ichnogeneric level, the lower Stormberg assemblage shares most of its members with assemblages from the Triassic of Europe and portions of the Newark Supergroup that predate the Late Norian (Ellenberger *et al.*, 1967, 1970). *Brachychirotherium* is unknown outside the Triassic and *Tetrasauropus* is too poorly known to be of any age-significance. *Grallator* spp. are universal through the Late Triassic and Early Jurassic. Three-toed, presumably dinosaurian footprints are very rare in Middle Triassic rocks (Demathieu, 1970). Finally, *Pentasauropus* may also occur in the Gettysburg Shale of the Newark Supergroup in an assemblage also containing *Brachychirotherium;* the age of that assemblage is Carnian-Norian, based on palynomorph assemblages (Cornet, 1977). In addition, if *Pentasauropus* was produced by a dicynodont, then it would again indicate a pre-Jurassic age. In summary, the determinate footprints of the lower Stormberg (i.e. *Brachychirotherium* and *Pentasauropus)* indicate a Late Triassic, probably pre-late Norian age, an assessment completely in line with the conclusions drawn from the skeletal material.

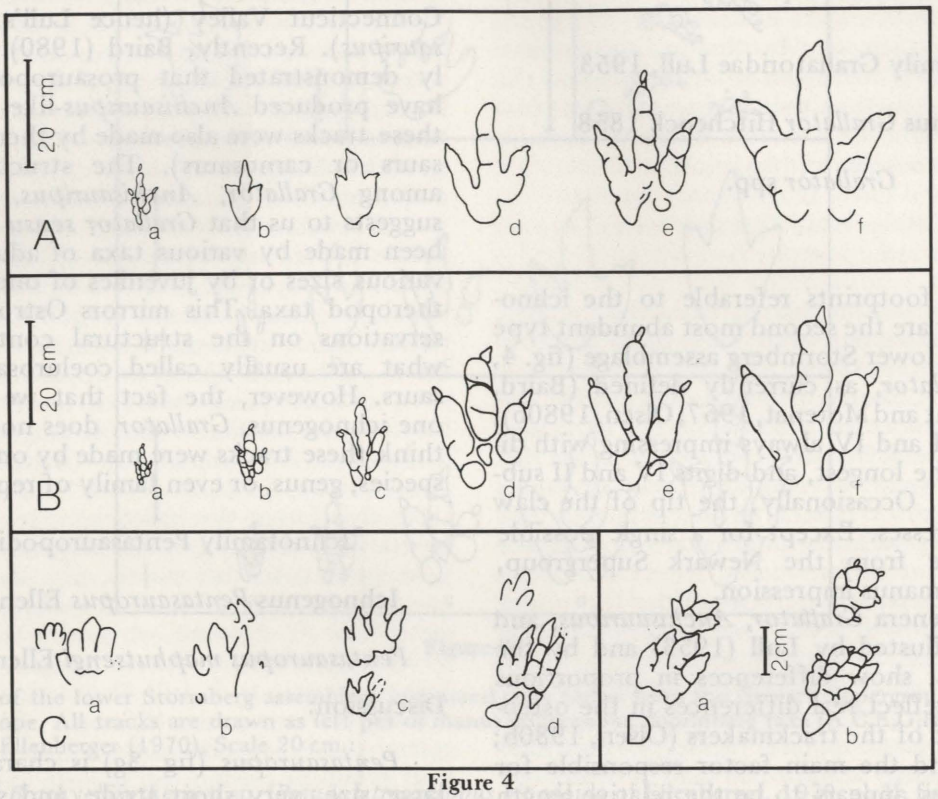

Figure 4

Tracks from the upper Stormberg assemblage compared with tracks from the Early Jurassic of the Newark Supergroup. Stormberg tracks traced from Ellenberger (1970 and 1974).

A) *Grallator* spp. from the upper Stormberg (all tracks redrawn as left pes impressions): a) *Grallator damanei* of Ellenberger 1970 (pl. VII, fig. 127); b) *Moyenisauropus palmipes* of Ellenberger 1970 (pl. VIII, fig. 68C); c) *Otouphepus palustris* of Ellenberger 1970 (pl. VII, fig. 94); d) *Neotrisauropus lambereshei* of Ellenberger 1970 (pl. VII, fig. 104b); e) *Kainotrisauropus morijiensis* of Ellenberger 1970 (pl. VII, fig. 125A); f) *Kainotrisauropus moshoeshoei* of Ellenberger 1970 (pl. VII, fig. 124B).

B) *Grallator* spp. from the upper Newark Supergroup (Early Jurassic)(all drawn as left pes impressions): a) type of *Grallator cursorius* of Hitchcock 1858 from the Portland Formation (Sineumurian – Toarcian) of the Hartford Basin, Massachusetts U.S.A. (original, A.C. 4/1); b) type of *Anchisauripus hitchcocki* of Lull 1904 from the Turners Falls Sandstone (Hettangian) of the Deerfield Basin, Massachusetts, U.S.A. (original, A.C. 56/1); c) type of "*Anchisauripus sillimani*" of Lull 1915 (= *Brontozoum sillimani* of Hitchcock, 1843) from Portland Formation (Toarcian) of Massachusetts, U.S.A. (original, same specimen as Hitchcock 1841, pl. 21); d) same as fig. 3, I, c of this paper; e) type of *Anchisauripus minusculus* of Lull 1904 from the Turners Falls Sandstone (Hettangian) of the Deerfield Basin, Massachusetts, U.S.A. (original, A.C. 16/1); f) same as fig. 3,1,d, of this paper.

C) Possible examples of *Batrachopus* spp. from the upper Stormberg (scale as in D and all drawn as right manus-pes sets): a) *Plateotetrapodiscus rugosus* of Ellenberger 1970 (pl. IX, fig. 81); b) *Suchopus bakoenaorum* of Ellenberger 1974 (pl. Q); c) *Molapopentapodiscus pilosus* of Ellenberger 1970 (pl. XI, fig. 116); d) *Synaptichnium motutongense* of Ellenberger 1974 (pl. Q) (mark indicated as digit IV in Ellenberger 1974 is omitted).

D) Type specimen of the type species of *Batrachopus, Batrachopus deweyi* Hitchcock 1843 according to Lull (1904) (original, A.C. 26/6) (drawn as right manus-pes sets): a) characteristic appearance of manus-pes impressions with less than the full complement of toes on the manus showing, and the pad underlying digit V of the pes not impressed; b) composite of all the information on the type slab, showing five toes on the outwardly directed manus and a pad under digit V on the pes.

Upper Stormberg (Upper Elliot and Clarens) footprint assemblage

The tracks from the upper Stormberg are at once more diverse and better preserved than those from the lower Stormberg. Absent are the brachychirotheriids and *Pentasauropus,* and in their place are tracks that were probably produced by a variety of dinosaurs and smaller non-dinosaurian forms.

Ichnofamily Batrachopodidae Lull 1904

Ichnogenus *Batrachopus* Hitchcock 1845

?*Batrachopus* spp.

Discussion:

Batrachopus (fig. 4) is the most abundant small, non-dinosaurian track in the late Norian (Rhaetian of Olsen and Galton, 1977) and Jurassic portions of the Newark Supergroup and seems to be represented in the upper Stormberg assemblage by a few of the ichnotaxa of Ellenberger (1974) (see Appendix). Unfortunately, as can be seen from Ellenberger's figures, the existing upper Stormberg material is too poorly preserved for a certain assignment to be made. *Batrachopus* can be thought of as a *Brachychirotherium* derivative, differing from the latter group by the reduction in the size and frequency of impression of the pad underlying digit V and the outward rotation of the five-toed manus impression (Colbert and Baird, 1958). The functionally tetradactyl pes and the outwardly rotated manus are characteristic of crocodiles (Deane, 1861; Baird, 1957; Haubold, 1971; Padian and Olsen, In Press; Schmidt, 1959). Because the majority of osteological pedal characters seen in crocodiles are also characteristic of other crocodiliomorphs (such as *Pedeticosaurus* and *Hallopus)*(Walker, 1968), it is likely that other crocodiliomorphs (such as sphenosuchids) as well as true crocodiles (such as protosuchids) could have made *Batrachopus*-like tracks. This agrees with Lull's (1904) suggestion that Newark *Batrachopus* were made by *Stegomosuchus,* first thought to be a thecodont, but now known to be a protosuchid crocodile (Walker, 1968).

In the Newark Supergroup, *Batrachopus* is often associated with the much larger and rarer *Otozoum.* Schmidt (1959) assigned *Otozoum* to the crocodiles, an opinion with which we agree. *Otozoum* is basically a "scaled up" version of *Batrachopus* (Baird, pers. comm.), but in contrast to its diminutive homeomorph, *Otozoum* rarely has manus impressions. Lull (1953) and Haubold (1971) have suggested that *Otozoum* was made by prosauropods; this is very unlikely because the manus impression indicates an osteological structure wholly unlike that of any known prosauropod, but like that of crocodiles.

Ichnofamily Grallatoridae Lull 1904

Ichnogenus *Grallator* Hitchcock 1858

Grallator (Grallator) spp., *G. (Anchisauripus)* spp., *G. (Eubrontes)* spp.

Discussion:

The most abundant type of track in the upper Stormberg assemblage, as in the Jurassic part of the Newark Supergroup, is *Grallator* spp. (fig. 5). The variety of *Grallator* forms in the upper Stormberg assemblage parallels the range seen in the Newark and, because the quality of much of the material is comparably good, we can confidently assign many of the upper Stormberg forms to Newark taxa as shown in our Figure 5. We reinterpret as marks extraneous to the trackways some of what Ellenberger (1970, 1972, 1974) interprets as extra digits in some of the tracks we refer to *Grallator* spp. Forms indistinguishable from Newark ichnospecies traditionally called *Anchisauripus sillimani, Anchisauripus minusculus,* and *Eubrontes giganteus* are present in the upper Stormberg assemblage, and we group these forms in *Grallator* spp. (fig. 5).

Like the *Grallator* tracks from the lower Stormberg assemblage, the upper Stormberg *Grallator* were probably produced by a variety of small to large theropod dinosaurs. The only definite theropod skeletal remains found in the Stormberg of the Karoo basin proper are fragments of the small theropod *Syntarsus* (Raath, 1980), known from much more complete and abundant remains from correlative beds in Zimbabwe (Raath, 1969). Despite its rarity in the Stormberg, *Syntarsus* makes a good match for the abundant upper Stormberg *Grallator (Anchisauripus)* sp. This is the reverse of the situation seen in the prosauropods of the upper Stormberg assemblage: prosauropods are by far the most common dinosaur, but there are no tracks, such as *Navahopus,* assignable to them in the upper Stormberg assemblage.

Cooper (1981: 797, fig. 89) considered that several of the ichnotaxa of Ellenberger (1970) from the Upper Stormberg fauna were made by the prosauropod *Massospondylus* but we refer these taxa to *Grallator (Kainotrisauropus morijiensis, K. moshoeshoei,* Fig. 4A; *Neotrisauropus deambulator)* or regard them as indeterminate (*Megatrisauropus malutiensis, Platysauropus* spp.) (see Appendix).

Ichnofamily Anomoepodidae Lull 1953

Ichnogenus *Anomoepus* Hitchcock 1848

Anomoepus spp.

Discussion:

Next to *Grallator,* tracks unmistakably belonging to the Jurassic Newark genus *Anomoepus* are the most abundant ichnites in the upper Stormberg assemblage (fig. 5). *Anomoepus* trackways are most often bipedal, but sitting or resting impressi-

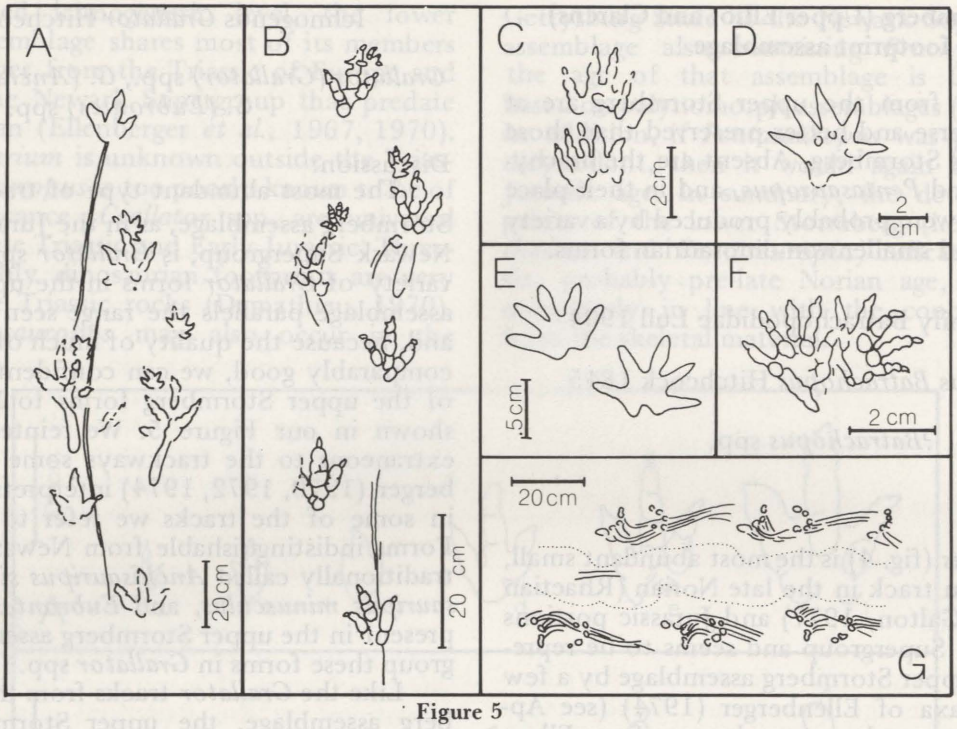

Figure 5

Tracks from the upper Stormberg assemblage, continued:

A) *Anomoepus* sp. from the upper Stormberg (*Moyenisauropus natator v. jejunus* of Ellenberger 1970 (pl. VI, fig. 64B).

B) type specimen of *Anomoepus intermedius.* Hitchcock 1865 (original, A.C. 48/1).

C and D) *Ameghinichnus* sp. from the upper Stormberg assemblage (C, *Aristopentapodiscus formosus* of Ellenberger, 1970, (pl. X, fig. 85A): D, *Eopentapodiscus mirabilis v. medius* of Ellenberger, 1970 (redrawn reversed from pl. IX, fig. 74A).)

E) *Ameghinichnus patagonicus* Casmiquela 1964 (left manus-pes set adapted from Bonaparte, 1978 and Casmiquela, 1964).

F) *Ameghinichnus* sp., left manus-pes set from the Towaco Formation (Hettangian) of the Newark Basin, New Jersey, U.S.A. (from Olsen, 1980c, fig. 20, E).

G) *Episcopopus ventrosus* Ellenberger 1970 from the upper Stormberg (from Ellenberger, 1975, pl. I).

ons in which all four feet are impressed, along with the metatarsi and sometimes the rump or belly, are common. *Anomoepus* tracks are often very detailed and, because of the large amount of information available from the trackways, they cannot be confused with other ichnotaxa. The pes is functionally tridactyl, with digits II, III and IV always impressed: digit I, which is larger than in *Grallator,* is sometimes impressed for its full length in sitting tracks and the tip of its claw often impresses even in walking tracks. The pes is broad and digits II, III and IV tend to be subequal in length with toes tending to be broadly splayed – much more so than in *Grallator.* In sitting or resting tracks there is often the impression of the metatarsus and the pes tends to be slightly less splayed than in fully walking tracks. The manus impression when present has four or five subequal toes and is sometimes rotated outwards. There are never big claws on the manus impression. The upper Stormberg forms we refer to *Anomoepus* (Table 3) not only match the Newark form in details of stance, gait, and anatomy, but also in the basic form of the resting impressions, which are unique among reptile trackways (fig. 5).

The five-toed manus with small claws, and the tetradactyl pes with digits II–IV subequal, indicates that small bipedal ornithischian dinosaurs were the likely makers of *Anomoepus* tracks. Among the skeletal forms from the upper Stormberg assemblage, the fabrosaurids are the best candidates. The other Stormberg ornithischians, the heterodontosaurids, can be ruled out because their manus is strongly modified, with elongated fingers that bear large claws (Santa Luca, 1980). Similarly, the manus of prosauropods, with the huge falciform claw on digit I, and the manus of theropods with their elongated phalanges and large claws, can be ruled out (*contra* Haubold, 1971). The structure seen in the manus and pes impressions of *Anomoepus* is very similar to that of the manus and pes in *Hypsilophodon, Scelidosaurus, Camptosaurus Tenontosaurus, Psittacosaurus,* and primitive ceratopsians. This general form may be primitive for ornithischians.

Ichnofamily Ameghinichnidae Casamiquela 1964

Ichnogenus *Ameghinichnus* Casamiquela 1964

Ameghinichnus spp.

Discussion:

Casamiquela (1964) named a series of quadrupedal five-toed tracks from the Middle Jurassic La Matilde Formation of Argentina *Ameghinichnus patagonicus*. A number of tracks from the upper Stormberg seem to be referable to that ichnogenus (Ellenberger, 1974) (fig. 5). *Ameghinichnus* is characterized by a five-toed manus and a five-toed pes which are subequal in size. The toes on both manus and pes impressions are subequal in length. In the type species of *Ameghinichnus* the manus is slightly smaller than the pes. Either the metacarpus and metatarsus are as short as or shorter than the phalanges, or the trackmaker was digitigrade (as Casamiquela believed). The pace is about equal to the stride in walking tracks, with the pes overstepping the manus in the type species (Casamiquela, 1964). The type material also includes galloping tracks. A form tentatively referred to *Ameghinichnus* has recently turned up in the Jurassic part of the Newark Supergroup of New Jersey (Olsen, 1980b; In Prep).

The five-toed subequal manus and pes of *Ameghinichnus,* both without an offset digit V, are not in themselves necessarily characteristic of any particular group. On the other hand, in the early Mesozoic and especially by the Early Jurassic, the variety of animals retaining this sort of foot structure was restricted to the last of the therapsid reptiles and the earliest mammals. The size of the larger of the upper Stormberg *Ameghinichnus* is greater than that of any known mammal of similar age, but the size of the smaller Stormberg tracks is about right for the largest Early Jurassic mammal, *Sinoconodon* (Hopson, pers. comm.). On the basis of their size and abundance, we suggest that tritylodontids are more likely candidates for the upper Stormberg forms and could have been responsible for the type material as well. Of course, skeletal material of tritylodontids is relatively abundant in the upper Stormberg.

Ichnofamily incertae sedis

Episcopopus Ellenberger 1970

Episcopopus ventrosus Ellenberger 1970

Discussion:

Sloppy quadrupedal tracks with a pace equal to the stride, a five-toed manus slightly smaller than the five-toed pes and a broad tail drag were named *Episcopopus* by Ellenberger (fig. 5). Superficially, these tracks resemble *Pentasauropus* from the lower Stormberg but differ in three ways: 1) the prominent tail drag; 2) the manus is slightly smaller than the pes; and 3) digits IV and V appear to be longest in the pes (or the foot was rotated medially during implantation). These features are not only different from *Pentasauropus* (justifying the generic difference), but also imply that *Episcopopus* and *Pentasauropus* were produced by very different animals. While *Pentasauropus* suggests a dicynodont, *Episcopopus* suggests a chelonian (as Ellenberger (1974) has pointed out). The chelonian known from the Stormberg is about the right size for *Episcopopus.*

There is at least a superficial similarity between *Episcopopus* and both the possible turtle tracks from the Upper Jurassic of Cerin, France (*Chelonichnium cerinense)* and the recent turtle tracks described by Berner, *et al.* (1982). Unfortunately, none of the tracks, including those of the living turtle, are really good enough to warrant detailed comparison with the equally muddled *Episcopopus.*

Age-significance of the upper Stormberg footprint assemblage

In the possession of small to large *Grallator* spp., small to large *Anomoepus* spp., ?*Batrachopus,* and *Ameghinichnus,* the upper Stormberg assemblages very closely resemble those of the Jurassic portions of the Newark Supergroup. The Jurassic age of the upper Newark is based principally on pollen and spores (Cornet, Traverse, and McDonald, 1973; Cornet and Traverse, 1975; Cornet, 1977; and Olsen, McCune, and Thomson, 1982) and on radiometric determinations of the interbedded and underlying lava flows (Olsen, McCune and Thomson, 1982). In the Newark, *Grallator* spp. occur throughout the Triassic and Jurassic portions, but the larger forms (*G. (Anchisauripus) minusculus* and *Grallator (Eubrontes)* spp.) occur only in the portion dated by pollen and spores as late Norian or younger (Rhaetian of earlier authors). *Batrachopus* is also restricted to beds dated as late Norian or younger. The assemblages from the late Norian portion of the Newark are virtually identical to assemblages from the "Rhaeto-Liassic" of France (Lapparent and Montenat, 1967). The only taxon represented by abundant material that distinguishes the early Jurassic of the Newark from the latest Triassic of the Newark or the French "Infraliassic" is *Anomoepus* (Olsen, 1980a), and this form is also abundant in the upper Stormberg. Despite scores of productive Triassic footprint localities from many Newark basins, *Anomoepus* has never been found in beds other than those dated by palynological or radiometric methods as Early Jurassic. A form described by Baird (1964) as *Anomoepus* from the Triassic (Carnian) Chinle Formation has proved on re-examination to be *Brachychirotherium* —Baird, pers. comm.). Likewise, *Ameghinichnus* although rare, is known only from Jurassic localities. Therefore, on the basis of the footprints alone, via correlation with the Newark Supergroup, the upper Stormberg assemblage is Early Jurassic in age.

IMPLICATIONS OF CORRELATION

Because the Stormberg contains two types of sediments usually thought of as palaeoclimatic indicators (coals in the Molteno Formation and dune sands in the Clarens Formation – Haughton, 1924), the redating of the Stormberg group has broad palaeoclimatic and biogeographic implications. Robinson (1971, 1973b) plotted the position of the palaeoclimatic indicators on a map of the position of the continents during the Triassic, and this figure has since been widely reproduced and quoted. However, the relative ages of virtually all of the North American and African Late Triassic and Early Jurassic deposits have been revised since 1973, so new maps are needed. Many of the paleoclimatic indicator deposits that were thought to be Late Triassic are now thought to be Jurassic, and new deposits of Triassic and Jurassic dune sands have been found; therefore, we provide two new maps (figs. 6 and 7), one for the Late Triassic (Carnian – early Norian) and one for the Early Jurassic (Hettangian – Pliensbachian). Also plotted on the Triassic map are the positions of localities that have produced certain fossils which show a latitude-dependent distribution. Biogeographic provinces are apparent in the maps for both the Triassic and Jurassic and these are reviewed below.

The Triassic (fig. 6)

Between north and south 30° latitude, phytosaurs and metoposaurs are abundant in Late Triassic (Carnian-Rhaetic) continental reptile assembla-

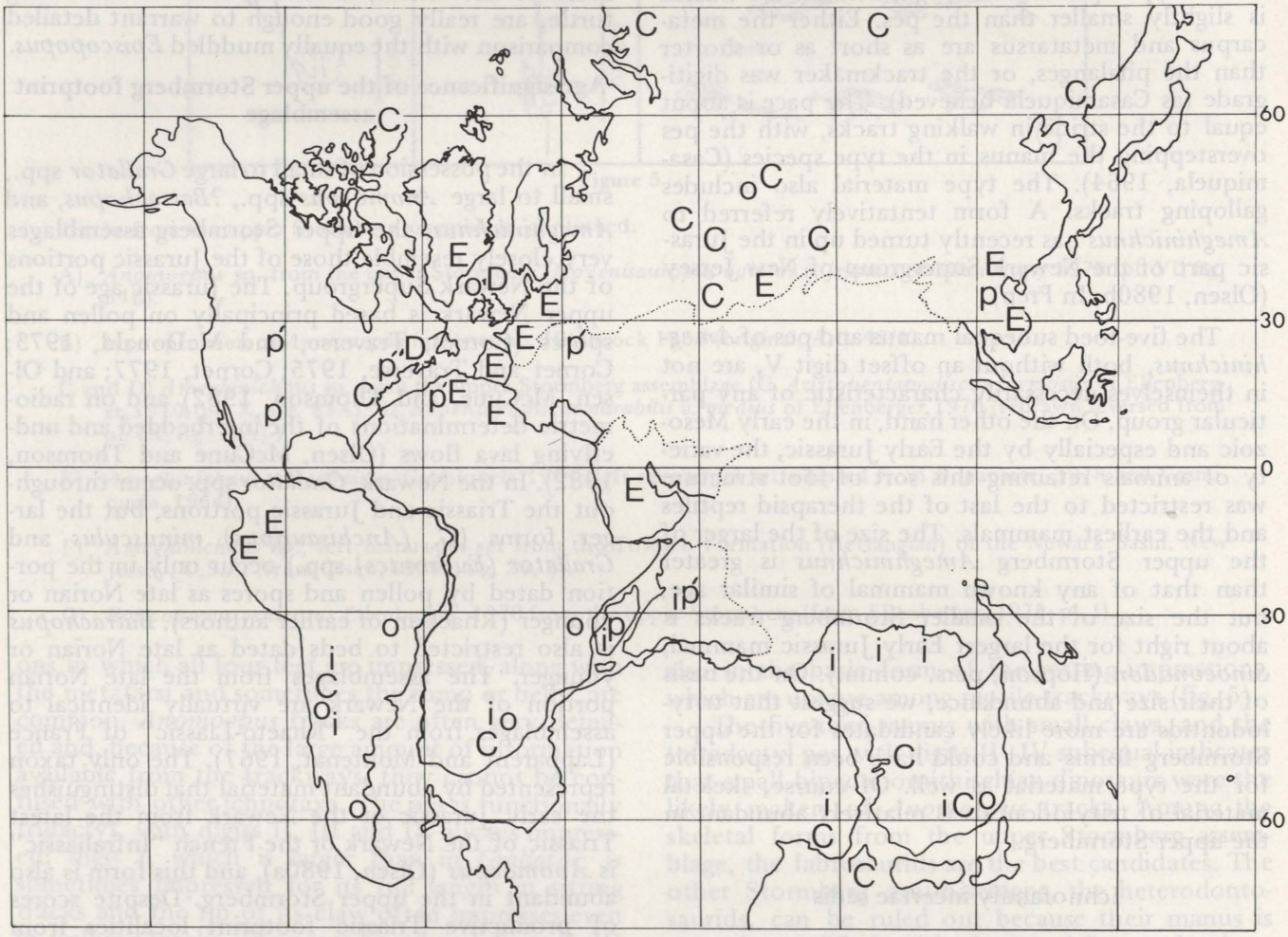

Figure 6

Position of the continents during the Late Triassic (Carnian–Norian) showing the occurrences of climate sensitive rocks (C, coals: D, dune sands; E, evaporites), the phytosaur-metoposaur province (p', phytosaurs and metoposaurs: p, only phytosaurs; o, good reptile assemblages but neither phytosaurs or metoposaurs), and the Gondwana floral province (i, Ipswich-Onslow microflora + *Dicroidium*-dominated macroflora).

Positions of most coals and dunes are from Robinson (1973), others from Hubert (1980), Olsen, McCune, and Thomson (1981), Anderson and Anderson (1971), and Haughton (1924); positions of evaporites are from Rona (1982) and Robinson (1973); phytosaur and metoposaur occurrences are from Olsen, McCune and Thomson (1981), Colbert and Gregory (1957), Colbert and Imbrie (1956), Roy-Chowdhury (1965), Dutuit (1979), Buffetaut and Ingavat (1982), and Westphal (1970). Occurrences without phytosaurs or metoposaurs are from Anderson and Anderson (1971), Robinson (1971), and Rozhdestvensky (1973). Distribution of the Ipswich-Onslow microflora and the *Dicroidium* macroflora from Dolby and Balme (1976), Anderson and Anderson (1971), and Kumaran and Maheswari (1980). Base map is from Smith (1981).

ges. In the early Late Triassic (Carnian), metoposaur amphibians are uniformly found in association with the phytosaurs. Phytosaurs and metoposaurs are found in abundance in Carnian age rocks in India (Roy-Chowdhury, 1965) and Morocco (Dutuit, 1977, 1979), as well as in continental Europe and eastern and western North America (Colbert and Gregory, 1967; Gregory, 1980; Jacobs and Murry, 1980). In addition, phytosaurs have also recently been found in Thailand (Buffetaut and Ingavat, 1982) and may be present in Malagasy (Westphal, 1970). Continental vertebrates are abundant in a number of South American basins in intervals which appear wholly to overlap the time span in which metoposaurs and phytosaurs lived elsewhere (Anderson and Anderson, 1971). While thecodonts in general and a variety of other labyrinthodont amphibians are abundant, phytosaurs and metoposaurs are absent. Likewise, the Molteno and lower Elliot appear to lack metoposaurs and phytosaurs, but again other thecodonts and labyrinthodonts are present (at least in the lower Elliot). Similarly, the Australian Late Triassic labyrinthodont-producing deposits lack phytosaurs and metoposaurs (Anderson and Anderson, 1971). Plotted on a map showing the position of the continents during the Late Triassic (fig. 6), the range of phytosaurs and metoposaurs appears to be restricted to the equatorial zone between North 40° and South 30° paleolatitude (see also Buffetaut and Ingavat, 1982). During the Late Triassic, India was south of the Tethys seaway (fig. 6). The presence of phytosaurs and metoposaurs in India shows that physical isolation by oceans of the southern continents cannot be used as a simple explanation for the absence of these herptiles from southern Africa and South America because they could clearly get to India, one of the most isolated segments of Gondwanaland at that time. It seems most likely that paleolatitude-dependant climatic differences were responsible for this provinciality.

The phytosaur-metoposaur biogeographic province closely follows (although not exactly) the contemporaneous plant provinces. In the Late Triassic southern hemisphere, south of 30°S paleo-

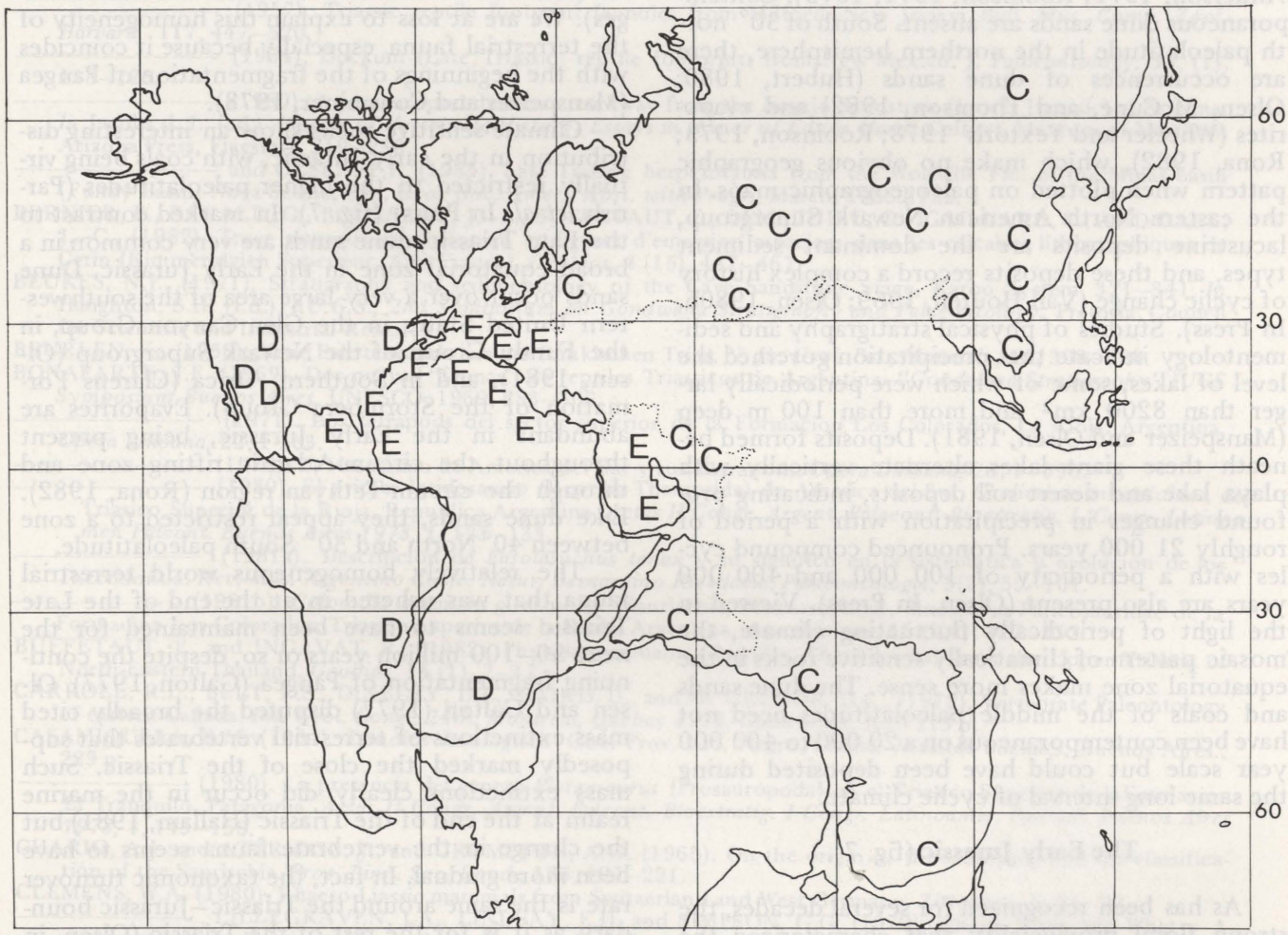

Figure 7

Positions of the continents during the Early Jurassic (Pliensbachian) showing the occurrences of "climate-sensitive" rocks (abbreviations as in fig. 6).

Occurrences of dune sands from Olsen (1981), Parrish, Parrish, and Ziegler (In Press), Haughton (1924), Cooper (1981b), and Cordani, Kawashita, and Filho (1978). Evaporite positions from Parrish, Parrish, and Ziegler (In Press) and Rona (1982). Positions of coals from Parrish, Parrish, and Ziegler (In Press). Base map from Smith (1981).

latitude, all vertebrate assemblages are associated with *Dicroidium*-dominated megafossil florules. Only in India are phytosaurs and metoposaurs found with a *Dicroidium*-dominated megafossil complex (Kumaran and Maheswari, 1980). In all other areas, the phytosaur-metoposaur province is associated with a typical bennetitalean-conifer assemblage. In addition, most of the extent of the southern hemisphere in which phytosaurs and metoposaurs are absent corresponds to the Ipswich-Onslow-type microfloras (Dolby and Balme, 1976; Truswell, 1980). In India, Onslow-type microflorules have been found in beds contemporaneous with the phytosaur-metoposaur bearing beds (Kumaran and Maheswari, 1980) and this parallels their association with *Dicroidium*. In the northern hemisphere, phytosaurs are absent from deposits north of about 30° N paleolatitude; however, this does not seem to correlate with any definite mega- or microfloral provinciality (Truswell, 1980).

Both in northern and southern paleolatitudes above 30°, coals are relatively common in the Late Triassic, particularly in the Carnian (Anderson and Anderson, 1971; Robinson, 1971, 1973). Contemporaneous dune sands are absent. South of 30° north paleolatitude in the northern hemisphere, there are occurrences of dune sands (Hubert, 1980; Olsen, McCune, and Thomson, 1982) and evaporites (Wheeler and Textoris 1978; Robinson, 1973; Rona, 1982), which make no obvious geographic pattern when plotted on paleogeographic maps. In the eastern North American Newark Supergroup, lacustrine deposits are the dominant sediment types, and these deposits record a complex history of cyclic change (Van Houten, 1969; Olsen, 1980b, In Press). Studies of physical stratigraphy and sedimentology indicate that precipitation governed the level of lakes, some of which were periodically larger than 8200 km² and more than 100 m deep (Manspeizer and Olsen, 1981). Deposits formed beneath these giant lakes alternate vertically with playa lake and desert soil deposits, indicating profound changes in precipitation with a period of roughly 21 000 years. Pronounced compound cycles with a periodicity of 100 000 and 400 000 years are also present (Olsen, In Press). Viewed in the light of periodically fluctuating climate, the mosaic pattern of climatically sensitive rocks in the equatorial zone makes more sense. The dune sands and coals of the middle paleolatitudes need not have been contemporaneous on a 20 000 to 400 000 year scale but could have been deposited during the same long interval of cyclic climate.

The Early Jurassic (fig. 7).

As has been recognized for several decades, the strong floral provinciality that characterized the Late Triassic world gave way in the Early Jurassic to a more homogeneous flora dominated in many areas by conifers (particularly the Cheirolepidaceae: Alvin, 1982). This is especially evident in the presumed pollen of the Cheirolepidaceae, *Corollina (Classopollis)*. Hughes (1973) has shown that in the Late Jurassic the relative abundance of *Corollina* is greatest in the equatorial region, and it appears that this pattern was first established in the Early Jurassic (Cornet, pers. comm.). Going from south to north in the circum-Atlantic rifting region, there is a clear trend from *Corollina*-dominated (+90%) (Cornet, 1977) to non-*Corollina*-dominated florules (– 10%) (Pederson and Lund, 1980) with transitional assemblages occurring around 25° North paleolatitude. This pattern is reflected in megafossils as well, with conifers strongly dominant in the south and much rarer in the north (Cornet, 1977; Pederson and Lund, 1980). The more northern assemblages are also far more diverse. In the southern hemisphere, data are as yet insufficient for a similar trend to be recognized, if it exists.

The relative homogeneity of the Early Jurassic world floras appears also in the faunas. Not only are the assemblages from different continents similar in taxonomic composition, with a series of genera being shared, but diversity is similar with the same taxonomic groups dominating the faunules (true for both the skeletal and track assemblages). We are at loss to explain this homogeneity of the terrestrial fauna, especially because it coincides with the beginnings of the fragmentation of Pangea (Manspeizer and Cousminer, 1978).

Climate-sensitive rocks show an interesting distribution in the early Jurassic, with coals being virtually restricted to the higher paleolatitudes (Parrish, *et al.* In Press) (fig. 7). In marked contrast to the Late Triassic, dune sands are very common in a broad equatorial zone in the Early Jurassic. Dune sands occur over a very large area of the southwestern United States in the Glen Canyon Group, in the Fundy Group of the Newark Supergroup (Olsen, 1981), and in Southern Africa (Clarens Formation of the Stormberg Group). Evaporites are abundant in the Early Jurassic, being present throughout the circum-Atlantic rifting zone and through the circum-Tethyan region (Rona, 1982). Like dune sands, they appear restricted to a zone between 40° North and 50° South paleolatitude.

The relatively homogeneous world terrestrial fauna that was ushered in at the end of the Late Triassic seems to have been maintained for the next 50–100 million years or so, despite the continuing fragmentation of Pangea (Galton, 1977). Olsen and Galton (1977) disputed the broadly cited mass extinctions of terrestrial vertebrates that supposedly marked the close of the Triassic. Such mass extinctions clearly did occur in the marine realm at the end of the Triassic (Hallam, 1981) but the change in the vertebrate fauna seems to have been more gradual. In fact, the taxonomic turnover rate is the same around the Triassic–Jurassic boundary as it is for the rest of the Triassic (Olsen, in prep). The apparent change that does characterize the transition into the Jurassic is a much reduced extinction rate in terrestrial vertebrates and perhaps this change is tied somehow to the reduction in regional provinciality.

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APPENDIX

All of Ellenberger's (1970, 1972, 1974) taxa are listed below in what we believe is correct synonymy. Discovery of better material may indicate that many of the taxa we group in the indeterminate category are in fact distinct and valid. The taxa are grouped first by whether they occur in the upper or lower Stormberg assemblage, second by the taxon with which they are synonymous, and third in alphabetical order. The date following the taxon name indicates either Ellenberger (1970) or (1974).

LOWER STORMBERG ASSEMBLAGE

Brachychirotherium Beurlen 1950
- *Deuterosauropodopus major* 1970
- *Deuterosauropodopus minor* 1970
- *Pseudotetrasauropus acutunguis* 1970
- *Pseudotetrasauropus angustus* 1970
- *Pseudotetrasauropus bipedoida* 1970
- *Pseudotetrasauropus dulcis* 1970
- *Pseudotetrasauropus elegans* 1970
- *Pseudotetrasauropus francisci* 1970
- *Pseudotetrasauropus mekalingensis* 1970
- *Sauropodopus antiquus* 1970
- *Tetrasauropus gigas* 1970
- *Tetrasauropus jacquesi* 1970
- *Tetrasauropus seakaensis* 1970

Tetrasauropus Ellenberger 1970
- *Tetrasauropus unguiferus* 1970

Grallator Hitchcock 1858
- *Deuterotrisauropus socialis* 1970
- *Qemetrisauropus minor* 1970
- *Qemetrisauropus princeps* 1970
- *Prototrisauropus angustidigitus* 1970
- *Prototrisauropus crassidigitus* 1970
- *Prototrisauropus graciosus* 1970
- *Prototrisauropus minimus* 1970
- *Prototrisauropus princeps* 1970
- *Prototrisauropus rectilineus* 1970
- *Prototrisauropus retilineus* (sic) 1970

Pentasauropus Ellenberger 1970
- *Pentasauropus erectus* 1970
- *Pentasauropus incredibilis* 1970
- *Pentasauropus maphutsengi* 1970
- *Pentasauropus morobongensis* 1970
- *Pentasauropus motlejoi* 1970

Indeterminate
- *Anatrisauropus ginsburgi* 1970
- *Batrachopodiscus curvus* 1970
- *Batrachopodiscus tsanatalani* 1970
- *Bosiutrisauropus phuthiatsani* 1970
- *Comptichnus moorosii* 1970
- *Dijaquesopus obliquus* 1970
- *Lacertoidopus sociabilis* 1970
- *Mafatrisauropus errans* 1970
- *Moltenotetrapodiscus vetus* 1970
- *Paratrisauropus equester* 1970
- *Paratrisauropus lifofanensis* 1970
- *Paratrisauropus mendrezi* 1970
- *Prototrisauropodiscus minimus* 1970
- *Pseudotrisauropus dieterleni* 1970
- *Pseudotrisauropus humilis* 1970
- *Pseudotrisauropus maserui* 1970
- *Pseudotrisauropus minusculus* 1970
- *Pseudotrisauropus molekoi* 1970
- *Pseudotrisauropus subengensis* 1970
- *Seakatrisauropus divergens* 1970
- *Seakatrisauropus unguiferus* 1970
- *Senqutrisauropus priscus* 1970
- *Trisauropodiscus aviforma* 1970
- *Trisauropodiscus galliforma* 1970
- *Trisauropodiscus levis* 1970
- *Trisauropodiscus phasianiforma* 1970
- *Trisauropodiscus popompoi* 1970
- *Trisaurpodiscus superaviforma* 1970
- *Tritotrisauropus medius* 1970

UPPER STORMBERG ASSEMBLAGE

Batrachopus Hitchcock 1845
- *Molapopentapodiscus pilosus* 1970
- *Molapopentapodiscus supersaltator* 1970
- *Nanopodiscus tenuis* 1970
- *Plateotetrapodiscus rugosus* 1970
- *Suchopus bakoeaorum* 1974

Grallator Hitchcock 1858
- *Aetonychopus digitigradus* 1974
- *Aetonychopus rapidus* 1974
- *Grallator damanei* 1970
- *Grallator matsiengensis* 1970
- *Grallator molapoi* 1974
- *Kainotrisauropus morijiensis* 1970
- *Kainotrisauropus moshoeshoei* 1970
- *Masitisisauropus angustus* 1974
- *Moyenisauripus palmipes* (C) v. *exiguus* 1970
- *Neotrisauropus deambulator* 1970
- *Neotrisauropus lacunensis* 1970
- *Neotrisauropus leribeensis* 1970
- *Neotrisauropus mokanametsongensis* 1974
- *Otouphepus magnificus* 1970
- *Otouphepus minor* 1970
- *Otouphepus palustris* 1970
- *Plastisauropus ingens* 1974
- *Sauroeidepus quthingensis* 1970

Anomoepus Hitchcock 1848
- *Kainomoyenisauropus* (cf. *Anomoepus*) *ranivorus* 1970
- *Masitisauropodiscus fringilla* 1974
- *Masitisauropodiscus turda* 1974
- *Masitisauropezus minimus* 1974
- *Masitisauropezus minutus* 1974
- *Masitisauropezus perdiciforma* 1974
- *Masitisisauropus palmipes* 1974
- *Moyenisauropus dodai* 1974
- *Moyenisauropus longicauda* 1974
- *Moyenisauropus minimus* 1970
- *Moyenisauropus minor* 1970
- *Moyenisauropus natalilis* 1974
- *Moyenisauropus natator* 1970
- *Moyenisauropus palmipes* 1970
- *Moyenisauropus vermivorous* 1970

Ameghinichnus Casmiquela 1964
- *Acropentapodiscus ginsburgi* 1970
- *Acropentapodiscus gracilis* 1974
- *Acropentapodiscus major* 1970
- *Ameghinichnus (?) gigas* 1970
- *Ameghinichnus parulus* 1970
- *Amphibiopus saltator* 1970
- *Aristopentapodiscus formosus* 1970
- *Aristopentapodiscus mirus* 1970
- *Calibarichnus cancrivorus* 1970
- *Dinopentapodiscus acutus* 1970
- *Dinopentapodiscus vandijki* 1970
- *Eopentapodiscus crassus* 1970
- *Eopentapodiscus intentus* 1970
- *Eopentapodiscus major* 1974
- *Eopentapodiscus mirabilis* 1970
- *Eopentapodiscus parvus* 1970
- *Grypopentapodiscus* (cf. *Aristopentapodiscus*) *fortis* 1970

Episcopopus Ellenberger 1970
- *Episcopopus ventrosus* 1970

APPENDIX (cont.)

UPPER STORMBERG ASSEMBLAGE

Indeterminate

Acropentapodiscus rapidus 1970
Arachnichus thabatsoeuensis 1974
Batrachopodiscus likhoelensis 1970
Batrachopodiscus quthingensis 1970
Cridotrisauropus cruentus 1970
Dipodiscus priscus 1970
Dinopentapodiscus lentus 1970
Dromicotetrapodiscus curvus 1974
Embrithopentapodiscus crassus 1970
Eodipodiscus insectiverous 1974
Eodipodiscus cf. priscus 1974
Eopentapodiscus crassus 1974
Eotetrapodiscus cursor 1970
Eotetrapodiscus moyensis 1970
Francipentapodiscus crassus 1970
Francipentapodiscus innoxius 1970
Francipentapodiscus medius 1970
Francipentapodiscus minor 1970
Francipentapodiscus minusculus 1970
Francipentapodiscus subtilis 1970
Gyrotrisauropus planus 1970
Kalosauropus masitisii 1970
Kalosauropus pollex 1970
Lehahichnus coquinaris 1970
Masitisauropus angustus 1974
Masitisauropus exiguus 1974
Masitisauropus cf. *exiguus* 1974
Masitisauropus levicauda 1974
Megatrisauropus malutiensis 1970
Mesodipodiscus pokanensis 1974
Microtetrapodiscus longifoma 1970
Molapopentapodiscus (Dipodiscus) saltator 1970
Moyenisauropodiscus perdiciforma 1970
Myopentapodiscus minusculus 1970
Myopentapodiscus (?) moorosii 1970
Myopentapodiscus tenuis 1970
Neotripodiscus makoetlani 1970
Otouphepus declivis 1970
Parapentapodiscus intentus 1974
Parapentapodiscus parvus 1974
Parapodiscus dubius 1974
Platysauropus robustus 1970
Platysauropus ingens 1974
Qomoqomosauropus acutus 1970
Sauroeidepus quthingensis 1970
Sauroeidepus matsepensis 1970
Synaptichnium motutongense 1974
Trisaurodactylus supervipes 1974
Trisauropodiscus supervipes 1970
Vandijkopentapus giantscastlensis 1970