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Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland

Farish A. Jenkins, Jr., Neil H. Shubin, William W. Amaral, Stephen M. Gatesy, Charles R. Schaff, Lars B. Clemmensen, William R. Downs, Amy R. Davidson, Niels Bonde and Frank Osbæck

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Instructions to authors.
See page 3 of cover.

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A diverse assemblage of fossil vertebrates has been discovered in the Fleming Fjord Formation (Malmros Klint and Ørsted Dal Members) in East Greenland between latitudes 71°15'N and 71°50'N. The fauna includes several species of mammals as well as prosauropod (*Plateosaurus*) and theropod dinosaurs, turtles (cf. *Proganochelys*), pterosaurs, aetosaurs (*Aetosaurus ferratus*, *Paratypothorax andressi*), labyrinthodont amphibians (*Gerrothorax*, *Cyclotosaurus* and possibly other taxa) and fishes (including sharks, actinopterygians, coelacanths and lungfish). The association of the genera *Aetosaurus*, *Plateosaurus*, *Proganochelys*, *Cyclotosaurus* and *Gerrothorax* is shared with well known European Norian faunas, and confirms the paleogeographic proximity of Greenland and Europe during Late Triassic time. On this evidence, the Ørsted Dal Member may be estimated to be at least as old as mid-Norian, but a comparable age estimate for the underlying Malmros Klint Member cannot be made on the basis of the fauna as presently known.

The Malmros Klint Member is characterized by composite cyclicity with four orders of cycles involving silt-rich, ephemeral lake or playa-mudflat systems, loess beds, wave-reworked sand flats, flat pebble conglomerates and paleosols. The rhythmicity and thickness ratios of the beds are evidence that depositional conditions were controlled by Milankovitch cycles, with climatic conditions varying from humid, to dry with seasonal rainfall, to arid. Cyclical sedimentary conditions and climatic fluctuations appear to have continued during the subsequent deposition of the overlying Ørsted Dal Member.

Key words:
Vertebrate paleontology, stratigraphy, sedimentology, Triassic vertebrate fauna.

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Introduction

Triassic sediments have long been known from East Greenland between latitudes 70°30'N and 74°30'N. The region is divisible into a northern sector, consisting mainly of the lowermost Triassic sediments of the Wordie Creek Formation, and a southern sector with a more complete representation of the Triassic section. Geographically, the southern area encompasses eastern

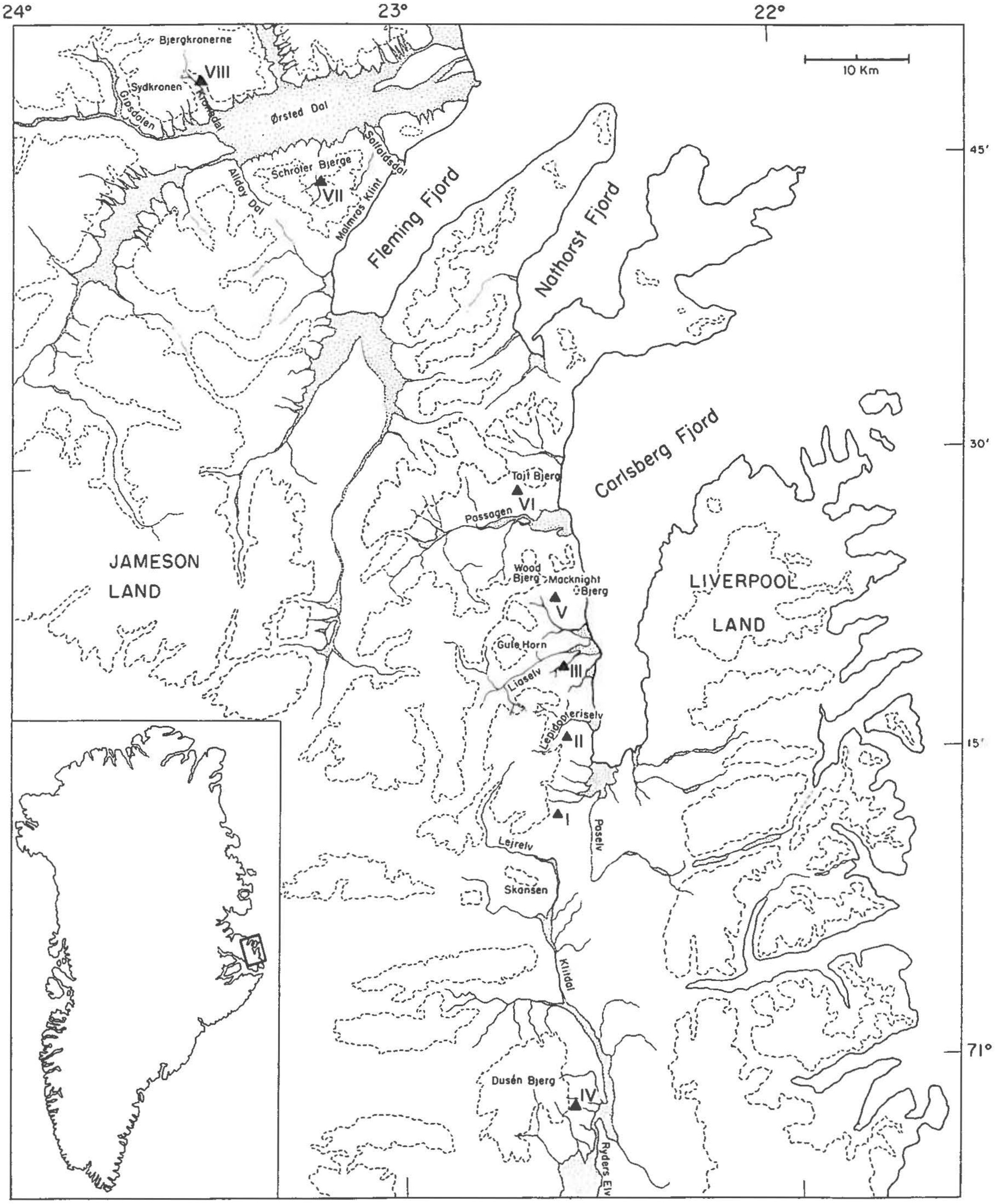


Fig. 1. Areas (I-VIII) in which exposures of the upper part of the Fleming Fjord Formation were surveyed for fossil vertebrates. Base camp coordinates of the most productive areas are as follows: II (Lepidopteriselv, 71°15.86'N, 22°32.37'W), V (Macknight Bjerg, 71°23.24'N, 22°34.34'W), VI (Tait Bjerg, 71°28.43'N, 22°40.43'W), VIII (Sydkronen, 71°49.65'N, 23°30.83'W). Based upon the Geodætisk Institut, Grønland series 1:250,000, Carlsberg Fjord quadrangle.

Scoresby Land, Jameson Land, Wegener Halvø and western Liverpool Land, and here the entire Triassic sequence, from the basal Wordie Creek Formation through the Pingo Dal and Gipsdalen Formations to the uppermost Fleming Fjord Formation (*sensu* Clemmensen, 1980a,b), is exposed.

Among the first to describe Triassic sediments in this region was O. Nordenskjöld (1907). A preliminary stratigraphic scheme proposed by Koch (1929) was subsequently modifed by Stauber (1942). Grasmück & Trümpy (1969) gave a detailed description of Triassic sediments in the southern sector where they estimated the composite thickness of the entire Triassic sequence to be on the order of 1800 m. Perch-Nielsen *et al.* (1974) redefined many of the units and proposed the currently used formal subdivision of the Triassic between Kong Oscars Fjord and Scoresby Sund. Clemmensen (1980a,b) further refined and subdivided the Scoresby Land Group based on a detailed lithostratigraphic study.

Few vertebrate fossils have been previously identified, and none described in detail, from the East Greenlandic continental Triassic, *i.e.* Pingo Dal, Gipsdalen and overlying Fleming Fjord Formations. Stauber (1942) noted a bone fragment from what is now recognized as the Vega Sund Member of the Gipsdalen Formation, and Grasmück & Trümpy (1969) found fish scales in the "Myalina limestones" now known as the Gråklint Beds, a middle unit within the Solfaldsdal Member of the Gipsdalen Formation (Clemmensen 1980b). From the Fleming Fjord Formation amphibian remains were found in the basal Edderfugledal Member (Clemmensen 1980b), and a capitosaurid palate, complete palaeonisciform fishes and scales of *Gyrolepis* were noted in the Malmros Klint Member (Clemmensen 1979). Vertebrate fossils have been consistently reported from the uppermost part of the Fleming Fjord Formation. Grasmück & Trümpy (1969, p. 55) observed that, "the dense and often bituminous, uppermost dolomite beds frequently contain abundant bone fragments, fish scales and a few reptilian teeth... This thin... bonebed has a very large distribution." Likewise, both Perch-Nielsen *et al.* (1972, 1974) and Clemmensen (1980b) noted this fossiliferous zone. Perch-Nielsen *et al.* (1972) reported a stegocephalian bone, a plesiosaur tooth, fragments of reptilian bones and ?*Gyrolepis* in the Ørsted Dal Member. Clemmensen (1980b) recorded fish remains (*Gyrolepis* and ?*Wimania multistriata*) and plesiosaur teeth at this level as well. Although these incidental observations provided some evidence of vertebrates in the Fleming Fjord Formation, the most important indicators were geological. Clemmensen's (1980a,b) description and interpretation of numerous lithofacies, together with studies reporting bioturbation that occurred under subaerial conditions (Bromley & Asgaard 1979), were consistent with conditions known elsewhere in which terrestrial vertebrates had been found. These studies formed the basis for the supposition that a paleontological reconnaissance in Jameson Land might demonstrate the presence of a significant vertebrate fauna in the Fleming Fjord Formation.

The primary goal of the field project was to explore the Fleming Fjord Formation of the Scoresby Land Group for fossil vertebrates and other evidence relating to the evolution of terrestrial tetrapod faunas during the Triassic-Jurassic transition. The intent was to pursue several problems. First, Late Triassic and Early Jurassic times witnessed important evolutionary transitions in the history of vertebrates. During the Late Triassic major tetrapod groups (mammals, dinosaurs, pterosaurs, crocodilians, turtles, among others), which were to continue to diversify throughout the Mesozoic, first appeared. Knowledge of the earliest representatives of these groups is thus critical to understanding their evolutionary origins. For this reason the survey was focussed on the Fleming Fjord Formation, and specifically the Malmros Klint and Ørsted Dal Members, which offered the most likely prospects in terms of both geochronology and outcrop exposure. Second, the continental earliest Jurassic is currently characterized, on basis of vertebrate faunas at least, primarily by the absence of "typical" Triassic taxa, a finding that has been interpreted as evidence of a major extinction event at the end of the Triassic (Olsen & Sues 1986; Olsen *et al.* 1987; Shubin & Sues 1991). Until recently, the dating of this extinction period was known only at a relatively coarse level of resolution; work in the Newark Supergroup of eastern North America, however, has led to the development of a more precise temporal scale on the basis of both biostratigraphic and paleomagnetic controls (Olsen 1986; Olsen & Kent 1990; Olsen *et al.* 1993). A more accurate correlation of other early Mesozoic continental sequences is therefore possible, but heretofore few data were available with which to assess the geochronology of the Triassic of central East Greenland.

In this paper we provide a survey of the Fleming Fjord vertebrate fauna as currently known, assess its geochronological and biogeographic significance, and offer an interpretation of the depositional environments in which the fauna was preserved.

Study area

Paleontological reconnaissance and collecting were undertaken in eight areas (I–VIII, Fig. 1) within the southern half of the Triassic rift basin as interpreted by Clemmensen (1980a). The majority of fossil vertebrates were found in areas II, V, VI and VIII; areas I and IV were largely unproductive. During the first three field seasons, locality data were recorded with reference to stratigraphic level and with approximate reference to base camp coordinates and/or local topographic features. In 1992 a Global Positioning System (Trimble Navigation, Ensign model) established detailed coordinate data for various localities.

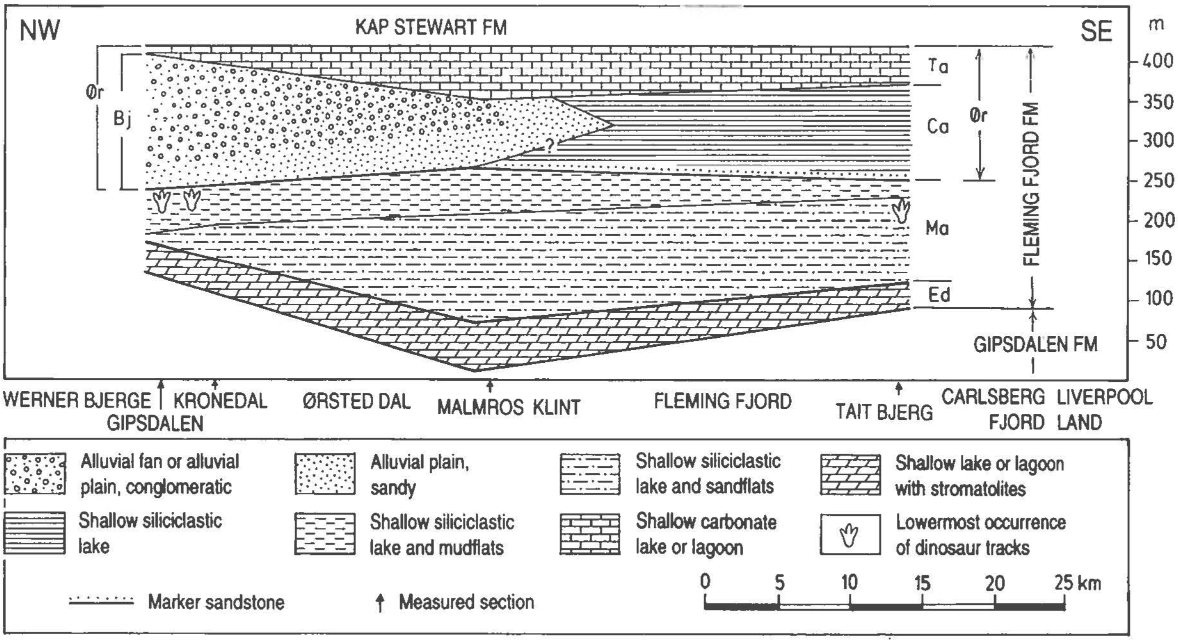


Fig. 2. Stratigraphy and depositional environments in the Late Triassic Fleming Fjord Formation, Jameson Land Basin, East Greenland. Ed = Edderfugledal Member; Ma = Malmros Klint Member; Ør = Ørsted Dal Member; Ca = Carlsberg Fjord beds (informal name); Bj = Bjergkronerne beds (informal name); Ta = Tait Bjerg Beds.

Stratigraphy

The Fleming Fjord Formation is composed of a basal Edderfugledal Member, a middle Malmros Klint Member and an uppermost Ørsted Dal Member (Fig. 2; Perch-Nielsen *et al.* 1974; Clemmensen 1980b).

The uppermost Ørsted Dal Member was subdivided into a basal siliciclastic unit (unnamed) and an overlying carbonate-bearing unit (Tait Bjerg Beds) by Clemmensen (1980b). Field studies of the basal siliciclastic interval undertaken during the present project indicate that this interval may be subdivided into a fine-grained siliciclastic unit towards the east (here informally termed the Carlsberg Fjord beds), and a more coarse-grained siliciclastic unit towards the northwest (here informally termed the Bjergkronerne beds) (Fig. 2).

Estimates of the age of the Fleming Fjord Formation had previously been based only on the rare occurrence of invertebrate fossils and palynomorphs. On this evidence, Grasmück & Trümpy (1969) and Clemmensen (1980b)

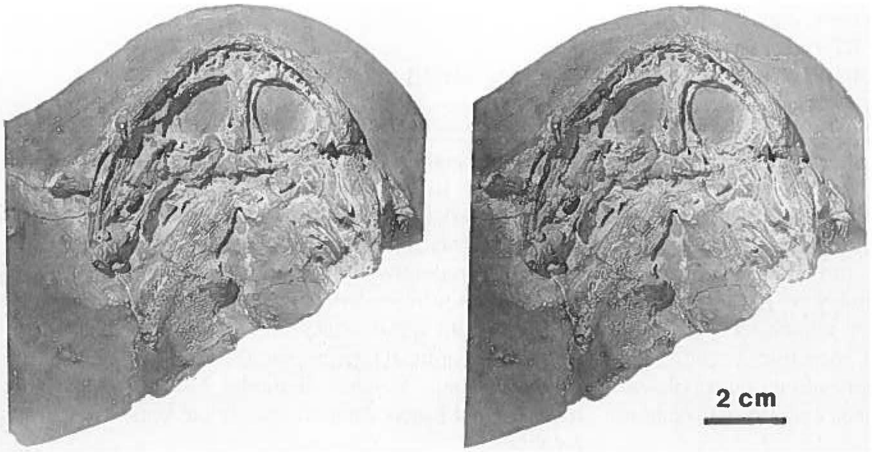


Fig. 3. Stereophotographs. Ventral view of a small skull of *Gerrothorax* cf. *pulcherrimus* (MCZ Field No. 21/91G) from the quarry (71°22.30'N, 22°33.14'W) at Macknight Bjerg.

Fig. 4. Dorsal view of the skull of a capitosaurid amphibian, *Cyclotosaurus* cf. *posthumus* (MCZ Field No. 15/92G), from the quarry (71°22.30'N, 22°33.14'W) at Macknight Bjerg.

suggested that the Fleming Fjord Formation spans most of the Carnian, Norian and Rhaetian.

Vertebrate taxa of the Fleming Fjord Formation

The taxonomic identities attributed to the Fleming Fjord vertebrates in this report are based on initial preparation and examination of specimens. For purposes of this faunal review, diagnostic features are listed for each taxon that support a preliminary identification, and some assessment is made, pending definitive descriptions of the material to be published separately, of the confidence level of each assignment.

Fig. 5. Ventral view of the capitosaurid skull shown in Fig. 4.

Plagiosaur (Amphibia: Temnospondyli) *Gerrothorax* cf. *pulcherrimus* E. FRAAS 1913

Material and occurrence. – Six skeletons and more than thirty-five variously complete skulls (Fig. 3) and/or jaws were found. The distinctively tuberculated dermal armor typical of Plagiosaurinae is the most commonly found, identifiable type of bone that occurs throughout the Ørsted Dal and upper part of the Malmros Klint Members in almost all of the surveyed areas. Plagiosaurine dermal armor occurs as isolated scraps *in situ* or is found as a component in lag deposits of fragmentary fish, amphibian and reptilian remains. The most complete plagiosaur material derives from a rich, localized bone assemblage in the lower part of the Carlsberg Fjord beds of the Ørsted Dal Member on the southern flank of Macknight Bjerg; an extensive quarry was made at this site (71°22.30'N, 22°33.14'W) where plagiosaurine amphibians were found to be the most common tetrapods of the taphocoenosis. Skull sizes range from 9.5–25 cm in breadth.

Diagnostic features. – Plagiosaurids are a group of

Triassic labyrinthodonts characterized by broad, greatly foreshortened skulls. Various cranial features have been interpreted by Shishkin (1987) as neotenic: the extremely large orbits, the extension of the parietals between the orbits and the resultant location of the pineal foramen in line with the posterior orbital margins, and the limited contact between the postparietal and supratemporal bones. The dermal ornamentation of small, bulbous tuberosities is characteristic of the later forms (Plagiosaurinae; Shishkin 1986a, 1986b, 1987). *Gerrothorax* is the most specialized of known plagiosaurids in cranial shape with a skull breadth 2.5 times the length; the triangular outline of the adductor fossa and the sparse number of small, vomerine teeth distinguish *Gerrothorax* from *Plagiosuchus* in which the adductor fossa is elongated and the numerous, tiny vomerine teeth form a prominent cluster (Romer 1947). The sutural relations of the parietal and supratemporal distinguish *Gerrothorax* from other genera that possess similarly foreshortened skulls. In *Gerrothorax* the parietal contacts the supratemporal broadly, whereas in *Plagiosternum* the contact is reduced to a point; in *Plagiosaurus* the bones are entirely separated by the intervening postfrontal and postparietal. Of the two described species of *Gerrothorax*, *G. rhaeticus* from the Rhaetic of Scania was described by Nilsson (1934, 1937, 1946) principally on the basis of postcranial elements; *G. pulcherrimus* from the Stubensandstein (Upper Keuper) of Pfaffenhofen, Württemberg, was originally assigned to the genus *Plagiosternum* by Fraas (1913b) and later reassigned to *Gerrothorax* by Nilsson (1937) who proposed diagnostic cranial and postcranial characters for the two species. According to Nilsson, *G. pulcherrimus* possesses a relatively straight posterior margin of the skull roof, a larger tabular that displaces more of the squamosal, a supratemporal that is well removed from the posterior margin of the skull, and a squamosal that projects anteriorly. These features, albeit relative in nature, appear to be represented in the Fleming Fjord plagiosaurids which therefore are tentatively assigned to *G. pulcherrimus*.

Cyclotosaur (Amphibia: Capitosauridae) *Cyclotosaurus* cf. *posthumus* E. Fraas 1913

Material and occurrence. – Isolated pieces of deeply sculptured dermal bone are common throughout the Ørsted Dal and upper part of the Malmros Klint Members in almost all of the surveyed areas. However, these pieces are diagnostic only as large temnospondyl amphibians. More complete but disassociated material is represented in the quarry (71°22.30'N, 22°33.14'W) at Macknight Bjerg: one large skull (Figs 4, 5), a smaller skull roof, jaws, vertebral centra and various limb elements. The largest known specimen, consisting of a fragmentary skull and associated partial mandibular rami from the uppermost Malmros Klint Member on the northern flank of Macknight Bjerg, is too incomplete for taxonomic determination. The marginal teeth of this specimen are anteroposteriorly compressed, and the palatal tusks measure between 28–34 mm in diameter at the base; an arcuate row of vomerine teeth is a feature shared with the skull illustrated in Figs 4 and 5.

Diagnostic features. – The following assessment of the most complete skull (Figs 4, 5) is made on the basis of characters selected from various sources (Welles & Cosgriff 1965; Paton 1974; Ingavat & Janvier 1981; Kamphausen & Morales 1981) which, it should be pointed out, differ in methodology and conclusions. Furthermore, we do not exclude the possibility that more than one large amphibian taxon is present in the Fleming Fjord fauna. Despite the fact that capitosaurs exhibit considerable morphological variation, and as a result their taxonomy is not well established (Jupp & Warren 1986), we assign the Fleming Fjord amphibian the genus *Cyclotosaurus* on the basis of the configuration of the otic and anterior palatal fenestrae, the shape of the choanae and cultriform process of the parasphenoid, the size of the orbits, and the relative contributions of bones forming the orbital margins. A closed otic fenestra distinguishes *Cyclotosaurus* from *Parotosuchus*, *Kestrosaurus* and *Mastodonsaurus* and other genera in which the otic notch is open posteriorly. In most species of *Cyclotosaurus*, the choanae are circular or slightly oval, and differ from the elongate choanae of *Stenotosaurus*, *Parotosuchus* and *Paracyclotosaurus*. In *Cyclotosaurus* the anterior palatal fenestra is single, not paired as in *Mastodonsaurus* and *Kestrosaurus* or absent as in *Paracyclotosaurus*, and the cultriform process of the parasphenoid is slender and keeled (not broad as in *Paracyclotosaurus*). The size and subcircular shape of the orbits of *Cyclotosaurus* are comparable to those of other capitosauroids except *Mastodonsaurus* in which the oval, relatively larger orbits are set close to the midline. The jugal contribution to the orbital border in *Cyclotosaurus* is approximately equal to that of the frontal, not greater as in *Parotosuchus* or excluded entirely as in *Stenotosaurus* (or *Eocyclotosaurus lehmani*, Kamphausen & Morales 1981).

The Fleming Fjord *Cyclotosaurus* appears to be identical to *C. posthumus* described by Fraas (1913b) from the Stubensandstein (upper middle Keuper) of Pfaffenhofen, Württemberg, and differs in several characters from other well established species. In *C. robustus* (from the Schilfsandstein, middle Keuper) the otic fenestrae are round, the length of the squamosal-tabular suture is about twice the diameter of the otic fenestra, the interpterygoid vacuity is broadest anteriorly, and the pterygoid-parasphenoid suture is short, whereas in *C. posthumus* the otic fenestrae are oval, the squamosal-tabular suture is approximately equal in length to the long axis of the otic fenestra, the interpterygoid vacuity is broadest in the middle, and the pterygoid suture with the parasphenoid is

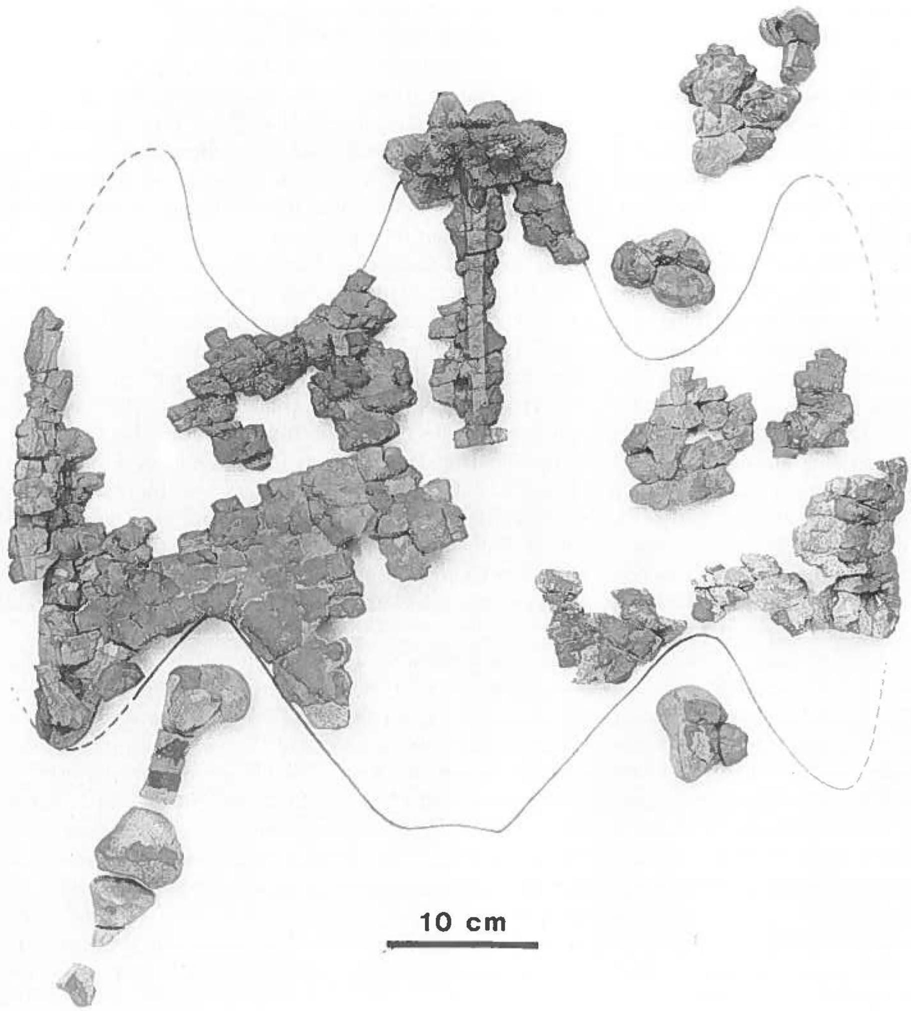


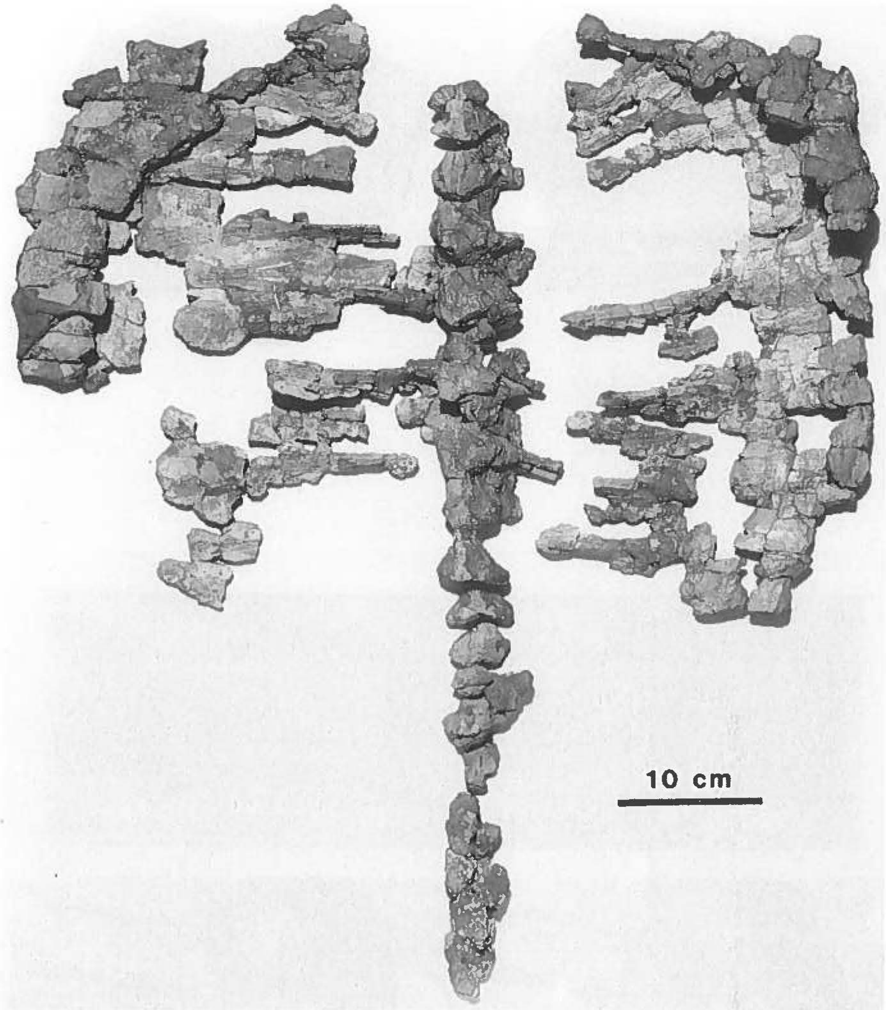
Fig. 6. Partial plastron, in dorsal view, and limb bones of a turtle, cf. *Proganochelys* sp. (MCZ Field No. 22/88G), from the Ørsted Dal Member, area II. The reconstructed margins of the plastron are shown outlined.

relatively long (Welles & Cosgriff 1965; Ingavat & Janvier 1981). Rounded choanae and a frontal that forms the major part of the anteromedial border of the orbit differentiate *C. posthumus* from *Stenotosaurus stantonensis* (lower Keuper, Staffordshire, England) in which the choanae are elongate and the frontal contributes little to the orbital margin. Oval otic fenestrae and parietals that terminate posterior to the transverse midline of the orbits differentiate *C. posthumus* from *C. ebrachensis* (middle Keuper, Blasensandstein) in which the otic fenestrae are round and the anterior end of the parietals do not reach the orbital midline. The Fleming Fjord cyclotosaur cannot be confidently distinguished from *C. hemprichi* (middle Keuper, Knollenmergel), a form that is apparently very similar to, if not conspecific with, *C. posthumus*. Most of the differences between the *C. posthumus* and *C. hemprichi* cited by Welles & Cosgriff (1965) are proportional or relative in nature, and fail to provide the basis for an unequivocal determination of the Fleming Fjord specimen.

Turtle (Chelonia: Proganochelyidae) cf. *Proganochelys* BAUR 1887

Material and occurrence. – A single specimen is represented by parts of the plastron and carapace, including both median (vertebral) and peripheral (marginal) elements, dorsal vertebrae, caudal vertebrae with partial osteoderms attached, the proximal and distal ends of a humerus, both proximal femora, a distal femur and other limb fragments (Figs 6, 7). The specimen, found in the upper part of the Ørsted Dal Member in area II (approximately 200 meters south of base camp II at 71°15.86'N, 22°32.37'W) was discovered on the surface of a deeply weathered zone that had also been subjected to solifluction. As a consequence the specimen was completely fragmented. Although it has been possible to reassemble portions of the skeleton, numerous unfitted pieces remain from what appears to have been a nearly complete post-

Fig. 7. Ventral view of the partial carapace of the same specimen shown in Fig. 6.



cranial skeleton. No cranial fragments have been identified.

Diagnostic features. – The anterior, median region of the plastron, consisting of the epiplastra and a partially preserved entoplastron (the clavicles and interclavicle, respectively), provides evidence of the taxonomic affinity of the Fleming Fjord turtle. The bases of the dorsal processes of the epiplastra, representing the clavicular diaphyses (Gaffney, 1985), are also preserved. Gaffney (1986) noted that the presence of dorsal processes alone is insufficient evidence to assign a fragmentary specimen to the genus *Proganochelys* because, in his opinion, it is a primitive character. The configuration of the margin of the anterior, median region of the plastron (Fig. 6), however, is comparable to that illustrated and discussed by Gaffney (1985, 1990) for *Proganochelys quenstedti* in which there are two pairs of cranially directed projections that supported gular and intergular scutes. In relative size and orientation the projections in the Fleming Fjord turtle appear to differ slightly from those in *Proganochelys quenstedti*; the epiplastral (lateral) projections in particular are more laterally directed, and the entoplastral (medial) projections appear relatively larger. The orientation of the epiplastral projections in the Fleming Fjord turtle more closely resembles that of *Proganochelys ruchae*, described by De Broin (1984) from the Late Triassic Huai Hin Lat Formation of Thailand. Although the incomplete preservation of the Fleming Fjord turtle in these and other features precludes a confident determination to the species level at present, pairs of gular and intergular projections are known only in *Proganochelys* (they are absent in *Proterochersis*, the only other Late Triassic turtle for which shell structure is known; Fraas, 1913a). On the basis of this evidence, it is reasonable to assign the Fleming Fjord turtle to the genus *Proganochelys.*

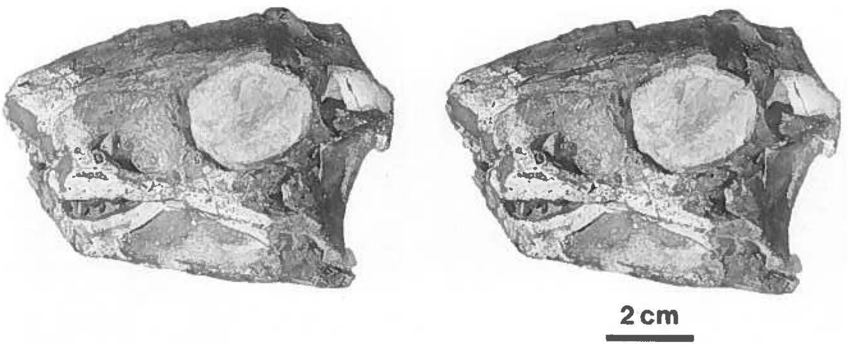


Fig. 8 Stereophotographs. Lateral view of a partial skull of an aetosaur, *Aetosaurus ferratus* (MCZ Field No. 22/92G), from the Ørsted Dal Member, area VIII.

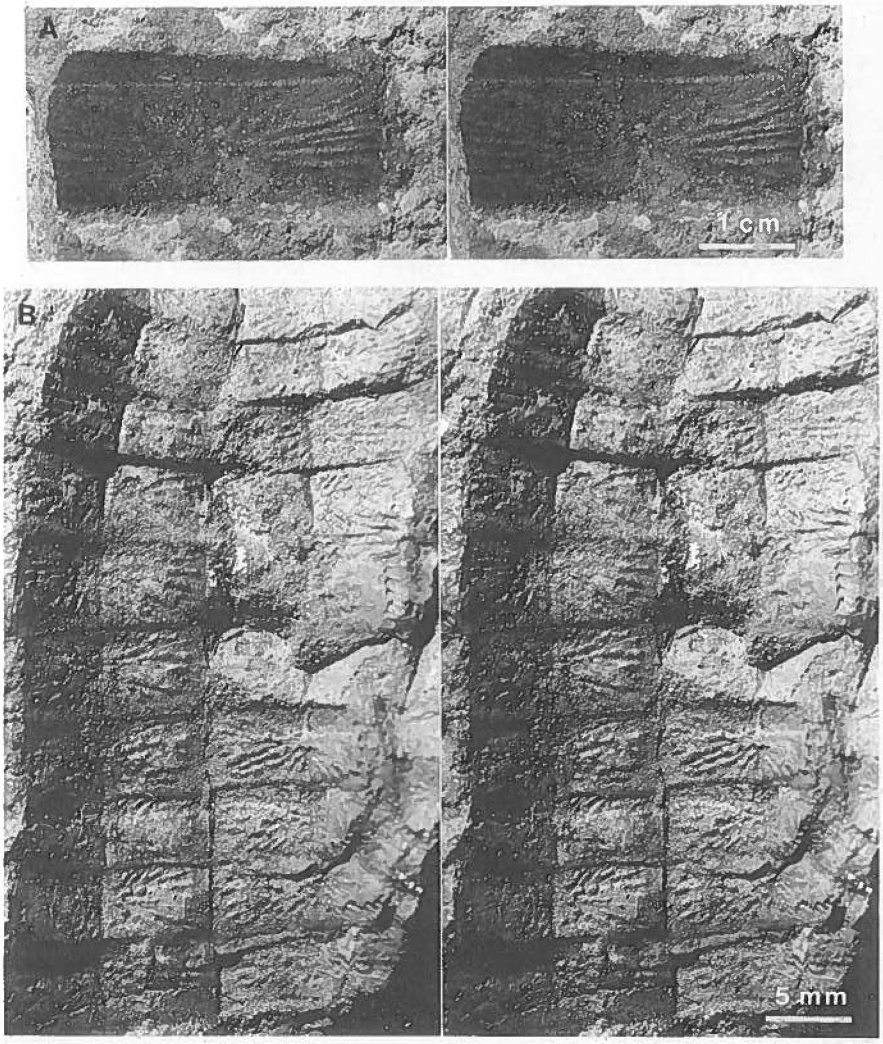
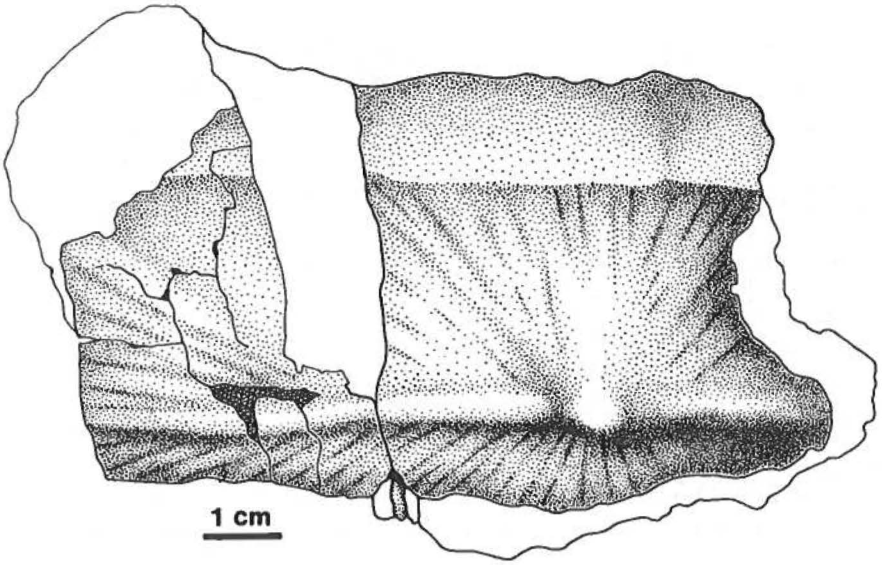


Fig. 9. Stereophotographs. Dermal armor associated with the aetosaur skull (MCZ Field No. 22/92G; Fig. 8). A, a paramedian scute. B, a series of articulated caudal scutes.

Fig. 10. A large paramedian scute with an ornamentation pattern characteristic of *Paratypothorax andressi* (MCZ Field No. 23/92G). Only a small amount of bone was preserved with the specimen which was represented for the most part as a mold of the scute. The natural mold was filled with epoxy and the matrix subsequently removed to provide a cast.



Aetosaurs (Archosauria: Stagonolepididae) *Aetosaurus ferratus* O. FRAAS 1877 *Paratypothorax andressi* LONG & BALLEW 1985

Material and occurrence. – Disarticulated, partial skeletons of two individuals (*Aetosaurus ferratus*) were quarried from a fluvial sandstone channel in the lower part of the Bjergkronerne beds of the Ørsted Dal Member in area VIII; elements represented are a nearly complete skull (missing the rostrum; Fig. 8), a partial maxilla with one tooth, lower jaw, humerus, femur, numerous vertebrae which include an articulated series of four vertebrae and a partial sacrum, and numerous dorsal, caudal and ventral dermal armor scutes. A third and much larger specimen (*Paratypothorax andressi*) consists of three partial dermal armor scutes (one paramedian, two laterals) that were found in skree blocks below the channel sandstone that yielded the two other specimens; the stratigraphic provenance is thus uncertain but is probably the Ørsted Dal Member.

Diagnostic features. – Among the most diagnostic features of aetosaurs are cranial structure (Walker 1961) and the ornamentation of the dermal armor (Long & Ballew 1985), and both lines of evidence indicate that the two partial skeletons represent *Aetosaurus ferratus*. In the skull (Fig. 8), the relatively small size of the temporal fenestra and large size of the orbit, the extensive contact between the postorbital and squamosal, and the configuration and orientation of the jugal are all features shared with *A. ferratus* as discussed and illustrated by Walker (1961). The tooth crowns in the Fleming Fjord aetosaur are bulbous and at the base slightly constricted; the enamel is faintly striated. The distinctiveness of *Aetosaurus ferratus* scute size and sculpturing (in contrast to that of its larger and younger sister species, *A. crassicauda*) has been recently reexamined by Wild (1989). The ornamentation of the scutes associated with the two Fleming Fjord specimens (Fig. 9) closely matches the radiating, oblong, closely appressed grooves on smooth-surfaced plates as described and illustrated by Wild (1989) for *A. ferratus*. The scutes range up to 49 mm in transverse width and 20.9 mm in anteroposterior breadth; although these dimensions are within the range of scute sizes given for a specimen of *A. crassicauda* (von Huene 1921), the sculpturing does not resemble the larger and more sparse sulci of this later appearing species.

The second aetosaur is a large form that may be referable to *Paratypothorax andressi* on the basis of the scute size and ornamentation. One scute of this specimen (Fig. 10), which is preserved as bone in part, the remainder as a cast, appears to be a left paramedian and measures in anteroposterior breadth approximately 50 mm, comparable to the breadth of scutes of the syntype of *P. andressi* (Long & Ballew 1985). The scute bears an eccentrically placed eminence and radiating groves that are most similar, among the large aetosaurs, to the pattern of *P. andressi*. Both the paramedian and two lateral scutes of the Greenlandic aetosaur distinctly resemble the dermal armor of *P. andressi* from the Chinle Formation, Petrified Forest National Park, Arizona (as illustrated by Hunt & Lucas 1992: Figs. 3B, 4A, B and by Lucas & Anderson 1993: Fig. 44D, G, I).

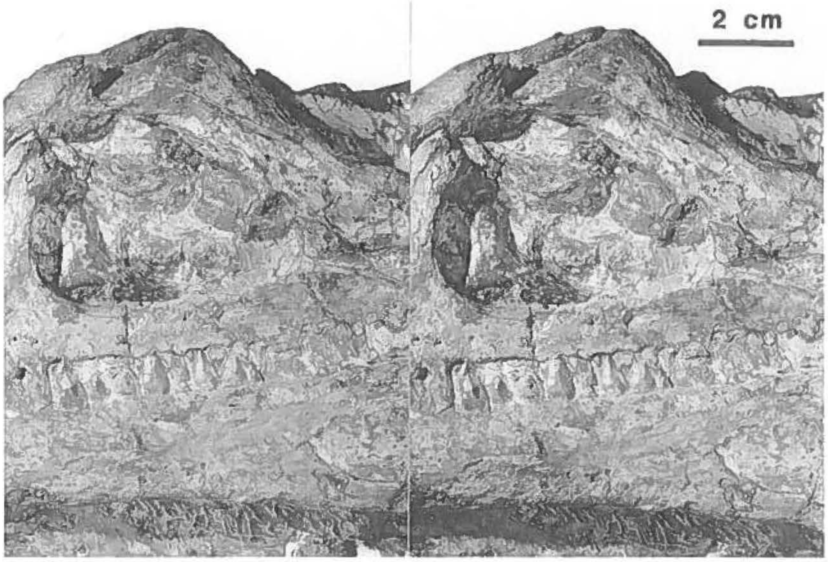


Fig. 11. Stereophotographs. Lateral view of the orbital region and mandibular dentition in a skull of a prosauropod dinosaur, *Plateosaurus engelhardti* (MCZ Field No. 61/91G), from the Malmros Klint Member on the north side of Macknight Bjerg (71°23.010'N, 22°34.114'W, elevation 335 m).

Prosauropod dinosaur (Saurischia: Prosauropoda) *Plateosaurus engelhardti* MEYER 1837

Material and occurrence. – One nearly complete adult skeleton; one complete skull and associated manus; three fragmentary specimens comprising various limb elements and vertebrae; two juvenile, partial skeletons, one including jaw fragments. Prosauropod remains were found in areas II, V, VI and VIII and occurred stratigraphically from the upper part of the Malmros Klint Member, principally in association with paleosols, to the uppermost part of the Carlsberg Fjord beds in the Ørsted Dal Member.

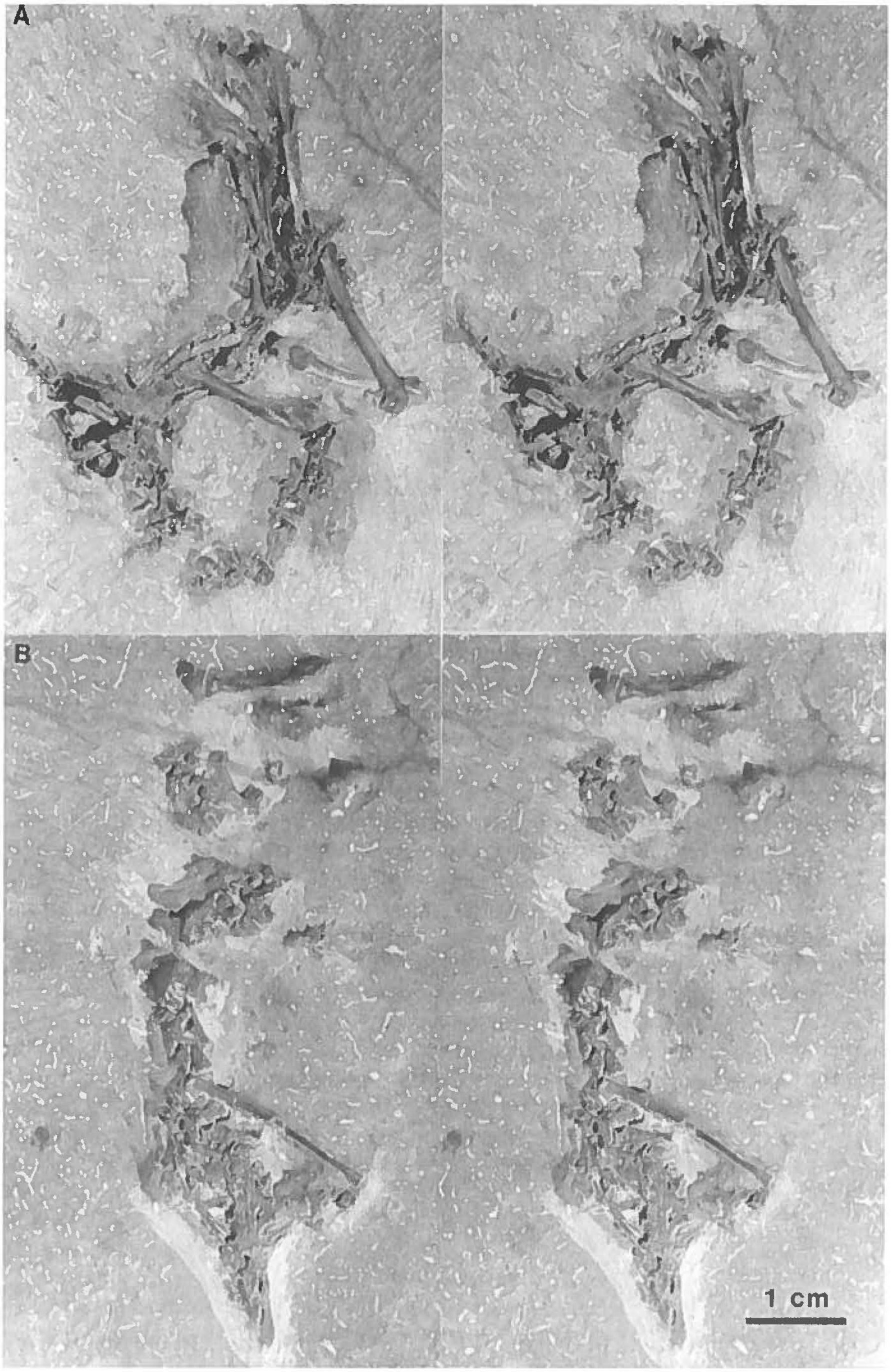
Diagnostic features. – Several features unequivocally establish these dinosaurs as prosauropods. The astragali, which are transversely broad and proximodistally compressed and bear a proximal process posterolaterally, are typical of a prosauropod pattern (Charig *et al.* 1965). The dentitions likewise show a suite of features characteristic of plateosaurids as well as other prosauropod families. The lanceolate teeth are set in an imbricating pattern, with the distal (posterior) edge of one tooth overlapping externally the mesial (anterior) edge of the following tooth; both mesial and distal edges of the teeth are serrated, with the serrations oblique to the cutting edge (Fig. 11). The generic identity of the Fleming Fjord prosauropods as *Plateosaurus* can be established on the basis of diverse features preserved in the Greenlandic materials that differentiate this taxon from other known prosauropods. Dental structure distinguishes *Plateosaurus* from the Lower Jurassic prosauropod *Massospondylus* (Attridge *et al.* 1985; A. W. Crompton & J. Attridge personal communication; Galton 1990). In adult *Plateosaurus*, there are 5 or 6 premaxillary teeth, 24–30 maxillary teeth, and the upper tooth row extends distally beyond the dentary row; in *Massospondylus* there are 4 premaxillary and 16 maxillary teeth, and the upper tooth row extends distally only as far as the end of the dentary row. In *Massospondylus* there is mesiodistal differentiation of teeth, and upper teeth are constricted at the base of the crowns; in *Plateosaurus* neither of these features occurs. *Plateosaurus* differs from the Lower Jurassic prosauropod *Anchisaurus* in having only a single dorsal process on the premaxilla and a Y-shaped quadratojugal, in contrast to *Anchisaurus*, in which the premaxilla has both dorsal and ventral processes and the quadratojugal is broadly L-shaped (A. W. Crompton & J. Attridge personal communication; Galton 1976). A subrectangular cross-section of the third sacral transverse process distinguishes *Plateosaurus* from *Sellosaurus gracilis*, from the lower and middle Stubensandstein, in which the cross-section is T-shaped (Galton 1984). Thus, on the basis of numerous features, the Fleming Fjord prosauropods may be confidently assigned to the monotypic genus *Plateosaurus*.

Theropod dinosaur (Saurischia: Theropoda)

Material and occurrence. – A single specimen from the upper Bjergkronerne beds in the Ørsted Dal Member on the western side of Sydkronen (area VIII) is represented by disassociated vertebrae and ribs, a partial pelvis and hindlimb, including a femur (length, 33 cm) and phalanges.

Diagnostic features. – Vertebral centra, which appear to be dorsals, are constricted in the middle relative to the cranial and caudal ends. The limb elements are slender

Fig. 12. Stereophotographs. Skeleton of a pterosaur (MCZ Field No. 13/91G), from the quarry (71°22.30'N, 22°33.14'W) at Macknight Bjerg. The specimen is preserved in two blocks (A, B) that separated along a cleavage plane.



and hollow. The distal phalanges, which are mediolaterally compressed and curved, would have supported trenchant claws. None of these features provides the basis for a specific identification, but taken together are indicative of a small, bipedal theropod dinosaur.

Pterosaur

Material and occurrence. – A single individual (Fig. 12) is represented by a nearly complete skeleton from the quarry (71°22.30'N, 22°33.14'W) at Macknight Bjerg. The rostral region of the skull, including a complete maxillary dentition, partial lower jaws, numerous ver-

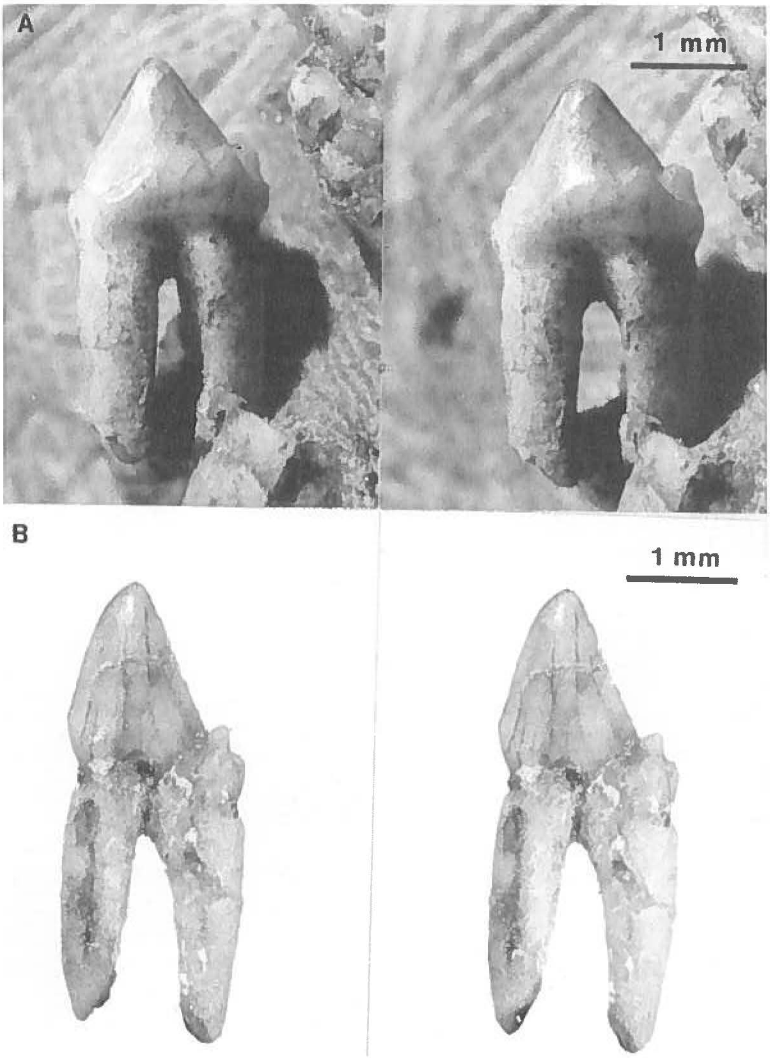


Fig. 13. Stereophotographs of mammalian teeth. (A) premolariform tooth (?left upper, in presumed buccal view, MCZ Field No. 62/91G No. 1). (B) premolariform tooth (?right lower, in presumed lingual view, MCZ Field No. 62/91G No. 2).

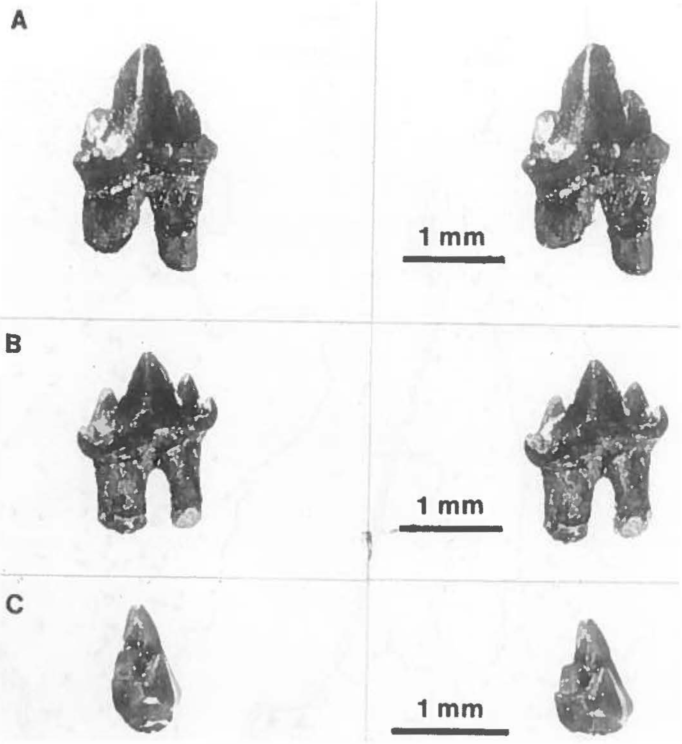
tebrae, fore- and hind limb elements are present. The particular importance of this specimen lies in the fact that the bones for the most part are uncrushed; the three-dimensional preservation contrasts with the flattened, planar preservation of most other early pterosaurian materials.

Diagnostic features. – In addition to the elongated phalanges and broad deltopectoral crest typical of pterosaurs, the dentition exhibits the distinctly heterodont condition of *Eudimorphodon* (Zambelli 1973; Wild 1984, figs. 5c, 6); especially characteristic are the tricuspid ("triconodont") maxillary teeth. However, there are sufficient differences in size, limb proportions and details of the dentition from those of *Eudimorphodon ranzii* to indicate that the Fleming Fjord pterosaur probably represents a new taxon.

Mammals *Kuehneotherium* KERMACK, KERMACK & MUSSETT 1968 (Kuehneotheriidae) cf. ?*Brachyzostrodon* SIGOGNEAU-RUSSELL 1983 (Morganucodontidae)

Material and occurrence. – Ten isolated teeth unequivocally document the presence of mammals as a faunal component in the upper part of the Fleming Fjord Formation. The specimens (all from area VI) were found at two stratigraphic levels and in different facies. Two premolariform teeth (62/91G No. 1, 62/91G No. 2; Fig. 13A, B)

Fig. 14. Stereophotographs of mammalian teeth. (A) buccal view of a left lower molariform tooth, *Kuehneotherium* sp. (MCZ Field No. 64/91G No. 8), showing well developed wear facets. (B) Molariform tooth (?upper left, in presumed lingual view), *Kuehneotherium* sp. (MCZ Field No. 64/91G No. 9). (C) Molariform (?lower left) tooth in distal view, cf. *Brachyzostrodon* sp. (MCZ Field No. 64/91G No. 4).



derived from a localized lag deposit, which included poorly sorted, fragmented reptilian, amphibian and fish remains, in lacustrine clastics 50 m above the base of the Carlsberg Fjord beds in the Ørsted Dal Member. The remaining eight teeth (64/91G No. 3–10) were preserved with a microvertebrate assemblage of predominantly disassociated bones in a dolomitic limestone at the top of the Fleming Fjord Formation (Tait Bjerg Beds).

Diagnostic features. – Five of the teeth, an incisor, a caniniform and three premolariforms, are not diagnostic for taxonomic purposes. The premolariforms are large (average crown+root height, 3.7 mm; average crown length, 1.7 mm) and are in the upper end of the size range expected for *Morganucodon* (Mills 1971) and other Rhaeto-Liassic mammals. The five molariform teeth, some of which are complete, indicate the presence of at least three taxa. Complete lower (crown length, 1.45 mm; Fig. 14A) and upper (crown length, 1.35 mm; Fig. 14B) molariform teeth represent a kuehneotheriid, probably *Kuehneotherium* itself, on the basis of the relative size and position of the cusps and the wear facets that record a distinctive occlusal pattern. The degree of angulation, or offset, of the accessory cusps with respect to the primary cusp on both teeth is less than that in the *Kuehneotherium* teeth originally described by Kermack, Kermack & Mussett (1968); variation in angulation is known, however, and we interpret both specimens as being relatively anterior in the molariform series. A second mammalian taxon is represented only by the distal half of a small molariform tooth (Fig. 14C). The presence of a very large internal cingular cusp (kuehneocone) is a distinctive characteristic of the morganucodontid *Brachyzostrodon* from lower Rhaetic deposits of Saint-Nicolas-de Port (Sigogneau-Russell 1983), but the Fleming Fjord specimen is smaller (estimated transverse width of the crown, 0.6 mm) than any of the lower molariform teeth of *Brachyzostrodon* described by Hahn, Sigogneau-Russell & Godefroit (1991). Additional taxa may be represented by two triconodont-like teeth. Although both are too incomplete for comparative purposes, one appears to have had a crown length of about 2.5 mm and is thus larger than those in most other known Late Triassic mammals.

Other vertebrate fossils

A number of additional taxa, mostly known from incomplete materials, are present in the upper part of the Fleming Fjord Formation. Fragmentary fish remains, especially scales, are common throughout the section in localized lenses. More complete fish remains occur in lag deposits with bone fragments of terrestrial vertebrates (at the quarry at Macknight Bjerg, for example), and include hybodont teeth and spines, teeth and jaws probably referable to *Saurichthys*, partial coelacanth skeletons and lungfish toothplates. Lungfish skulls are present beneath

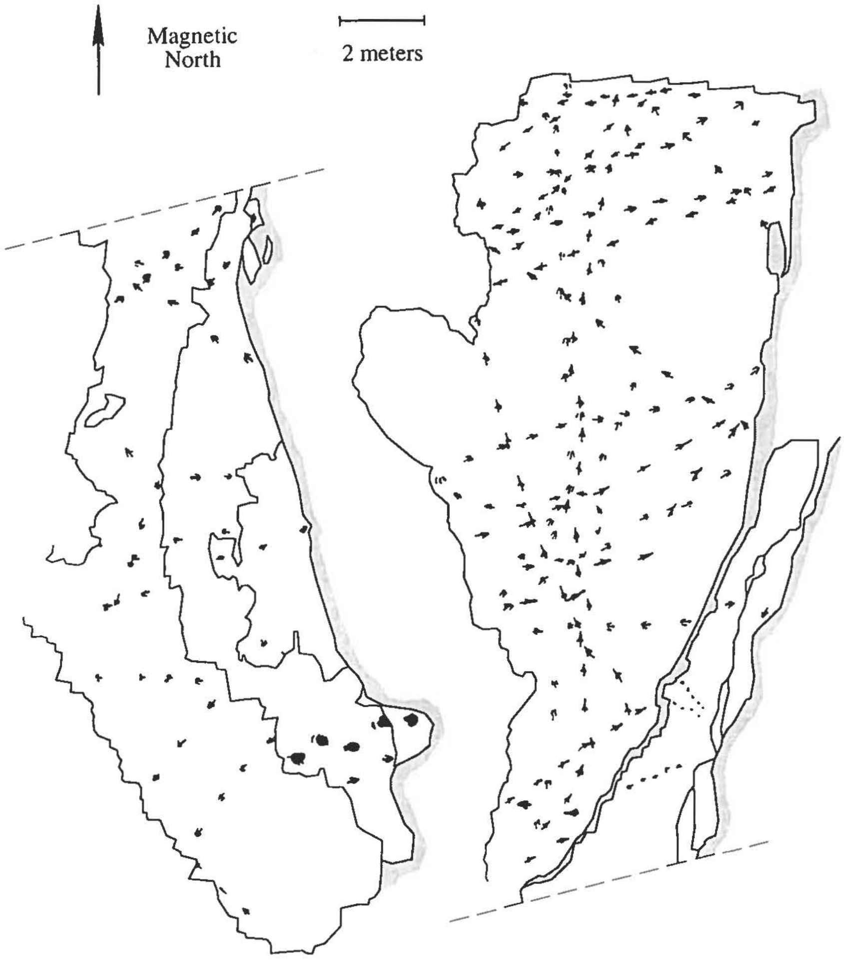


Fig. 15. Map of the dinosaur trackways at 71°24.88'N, 22°33.17'W (elevation 536 m) on the eastern slope of Wood Bjerg (see Fig. 1). Prepared by Stephen M. Gatesy.

mud-cracked beds in the Ørsted Dal Member south of Liaselv (area III).

Fragmentary cranial and postcranial materials recovered from the Malmros Klint Member (area V) may represent a phytosaur; the tentative identification is based on the circular cross-section of the teeth and the pyramidal shape of a single, associated scute.

A few fragments of a large reptilian carnivore (area II), comprising a piece of the jaw and impressions of a serrated tooth (crown length approximately 1.6 cm), partial limb bones, ribs and vertebrae, possibly represent a rauisuchid.

Jaw fragments characteristic of sphenodontians and ?lepidosaurs were found in association with the mammalian taxa described above.

Footprint assemblages

Material and occurrence. – Vertebrate footprints occur throughout the upper part of the Fleming Fjord Formation. Tracks are most common and best preserved on thin (ca. 10 cm), laterally extensive beds of fine grained clastics in the Carlsberg Fjord and lowermost Tait Bjerg Beds of the Ørsted Dal Member. The greatest concentration of trackways is found in area V on the eastern shoulder of Wood Bjerg (at 71°24.88'N, 22°33.17'W, elevation 536 m) where several track-bearing bedding planes have been extensively exposed (Fig. 15). The most abundant are three-toed footprints (4–28 cm in length) assignable to *Grallator* spp. (cf. Olsen & Galton 1984). No prints of a manus have been identified with any tridactyl trackway. Until evidence is found to suggest otherwise, these are attributed to small to medium-sized theropod dinosaurs. A second type are elongate tracks (21–44 cm in length) with impressions of the metatarsus and digit I in addition to digits II, III and IV, providing evidence of plantigrade locomotion in these bipeds. Skin impressions have been found at the Wood Bjerg site and two other localities (area VI); conspicuous tail drag marks occur on one layer. Based on a sample of footprint orientations (N=57) from several localities, dinosaurs were primarily moving towards the NE, SW and SE; only a few trackways are headed NW.

Three trackways consist of large, approximately circular prints (36–53 cm in diameter). In the best preserved example the impressions of four clawed digits, oriented anterolaterally, are visible; small, crescentic impressions of the manus are also present. These prints are suggestive of a large, quadrupedal archosaur.

Trackways of much smaller quadrupeds occur in the Ørsted Dal Member in several areas. Finally, imprints (2.5–5 cm) of the volar surface and four relatively short digits with rounded ends occur in the Malmros Klint; these are probably amphibian in origin.

Biostratigraphic and geochronologic implications

Two general interpretations may be made from the East Greenlandic fossil vertebrate fauna as recognized to date. First, the fauna is predominantly European in aspect, in agreement with similarities established on the basis of fossil plants (Harris 1937, 1961). Second, the fauna is indicative of a Norian age for at least the upper part of the Fleming Fjord Formation. The taxa that may be cited in support of these interpretations are discussed below. Most fossil vertebrates were collected from the uppermost Malmros Klint and the overlying Carlsberg Fjord beds of the Ørsted Dal Member; the lower part of the Fleming Fjord Formation could possibly be Carnian.

Prosauropods are ubiquitous in terrestrial faunas of the Late Triassic and Early Jurassic and have been found on all continents, including Antarctica. Complete skeletons and skulls are relatively rare, however, and for this reason the Fleming Fjord *Plateosaurus* specimens are important. The earliest known records are Carnian (lower Upper Triassic; Morocco and possibly South Africa); the latest forms are Pliensbachian/Toarcian (upper part of the Lower Jurassic, Connecticut and Arizona, USA; Galton 1985a, 1990). Although the genus *Massospondylus* appears to have achieved wide distribution (Africa, North America) in the Early Jurassic (Attridge *et al.* 1985), there is little evidence that other known genera were widespread geographically or geochronologically. The genus *Plateosaurus* is best known from materials from the Knollenmergel (upper middle Keuper, Norian) of Europe but its range extends to the end of the Triassic (upper Keuper, Rhaetian; Galton 1985b, 1986, 1990). The presence of *Plateosaurus* in the upper part of the Fleming Fjord Formation may be taken as one line of evidence supporting a Norian age for the Ørsted Dal and uppermost part of the Malmros Klint Members. Indeed, given Greenland's proximity to Europe as part of the Laurasian land mass during Late Triassic times, the shared occurrence of *Plateosaurus* and other taxa is hardly surprising.

The earliest known turtles are of Late Triassic (mid-Norian) age and are represented by two taxa from the German Keuper. *Proganochelys quenstedti* from the Stubensandstein and Knollenmergel is known from both cranial and postcranial material, whereas the pleurodire *Proterochersis robusta* from the Stubensandstein is known from shells only (Fraas, 1899, 1913a; Gaffney, 1986). Fragmentary remains of a proganochelyid from Thailand have been described (De Broin *et al.* 1982; De Broin 1984) in association with a Norian fauna of plants, ostracods, semionotids, lungfish, *Cyclotosaurus* sp., and phytosaurs. A proganochelyid skull from the Elliott Formation ("Red Beds") of South Africa has yet to be described, and may be either of Late Triassic or Early Jurassic age (Gaffney, 1986). However, no proganochelyid is definitely known from post-Triassic time; the Fleming Fjord chelonian, if substantiated as *Proganochelys*, establishes another correlative link with Norian deposits of Europe.

Aetosaurs are represented by some eight genera from deposits of Late Triassic age in North and South America and Europe, and some species appear to be useful geochronological indicators. *Aetosaurus ferratus* is known from the lower Stubensandstein of both Stuttgart-Kaltental and the Stromberg Mountains in northern Württemberg, and is also known from the Calcare di Zorzino (Zorzino Limestone) in the Upper Triassic sequence of Cene (Lombardian Alps, northern Italy) that Wild (1989) considered middle Norian. Tintori & Sassi (1992) assigned the Zorzino Limestone an age of middle late Norian, but recent palynological evidence (A. Tintori, F. Jadoul & S. Cirilli personal communication, 1994) indicates that the Zorzino fauna spans the Alaunian-Sevatian boundary (*i.e.* between middle and late Norian). The precise stratigraphic range of *A. ferratus* remains uncertain; there is no evidence of *A. ferratus* below the lower Stubensandstein, and this species is apparently succeeded by *A. crassicauda* in the middle Stubensandstein, which is likewise considered middle Norian (Wild 1989). The occurrence of *A. ferratus* in the lower part of the Bjergkronerne Beds in the Ørsted Dal Member is therefore suggestive evidence that the Ørsted Dal Member is at least as old as the earliest part of the late Norian and may well extend into the middle Norian.

The apparent presence of *Paratypothorax andressi* in the Fleming Fjord Formation represents a correlative link between Europe, where this species is found in the lower Stubensandstein of Stuttgart-Heslach (Württemberg), and North America, where the same species occurs in the Chinle, Bull Canyon and Dockum Formations of Arizona, New Mexico and Texas (Long & Ballew 1985; Hunt & Lucas 1992). Long & Ballew (1985) interpret the age of the North American occurrences as being late Carnian/?early Norian. Hunt & Lucas (1992) specifically date the North American *Paratypothorax* as ranging between late Carnian and early Norian, whereas they assign the European occurrence as being somewhat later in the early Norian, contra Wild (1989) who cited the lower Stubensandstein as middle Norian.

The Fleming Fjord amphibians add further evidence for a Norian age of the upper Malmros Klint and Ørsted Dal Members. Although plagiosaurids occur throughout the Triassic and have been found in Europe, Asia and Australia (Shishkin 1967, 1986b; Warren 1985), species of *Gerrothorax* have only been reported from the middle part of the so-called "Rhaetic" layers in Scania (Nilsson 1934, 1937, 1946; *G. rhaeticus*) and from the Stubensandstein of Pfaffenhofen, Württemberg (Fraas 1913b; von Huene 1922; Nilsson 1937; *G. pulcherrimus*). Similarly, among capitosaurids, which range throughout the Laurasian Triassic, a closely related group of *Cyclotosaurus* species (*C. robustus*, *C. ebrachensis*, *C. hemprichi*, *C. posthumus*) are all from the middle or upper Keuper (Welles and Cosgriff 1965; Ingavat & Janvier 1981). The apparent presence of *Gerrothorax pulcherrimus* and *Cyclotosaurus posthumus* in the upper part of the Fleming Fjord Formation duplicates their co-occurrence in the Stubensandstein (upper middle Keuper).

Among early pterosaurs, the most complete specimens are from deposits of Norian age in northern Italy, and are represented by the relatively advanced genus *Eudimorphodon* as well as such primitive forms as *Peteinosaurus* and *Preondactylus* (Zambelli 1973; Wild 1978, 1983, 1984). Fragmentary pterosaurian material, including isolated teeth referrable to *Eudimorphodon*?, have also been reported from North America in the Late Triassic Dockum (Murry 1986) and possibly in the Chinle Formation as well (Jacobs & Murry 1980). Murry (1989) subsequently noted that a mandibular fragment and an incomplete maxilla from the Dockum were comparable to that in *Eudimorphodon*; on the basis of palynological data, he interpreted the Dockum material as Carnian in age. The presence of a pterosaur in the Greenlandic Late Triassic lends further credence to Fraser & Unwin's (1990) contention that the initial radiation of this group took place during the Triassic, rather than in the Jurassic as had been previously generally believed.

The preponderance of vertebrate faunal evidence thus favors a Norian age for at least part of the upper Fleming Fjord Formation. It is not possible on the basis of the known stratigraphic distribution of taxa to determine whether the uppermost part of the Ørsted Dal Member (*i.e.*, Tait Bjerg Beds) is Rhaetic, or to what extent the Malmros Klint Member may extend into the Carnian. On the basis of diverse evidence, Olsen *et al.* (1993) estimate the Triassic-Jurassic boundary to be at approximately 201.5 Ma, the Rhaetian-Norian boundary at 207–208 Ma, and the Carnian-Norian boundary at 217 Ma. If the Fleming Fjord vertebrate fauna is recognized as equivalent to that of a Stubensandstein-Knollenmergel assemblage, and thus middle to late Norian, we hypothesize the age of this fauna to be approximately 208–212 Ma.

Despite these uncertainties, the documented association of mammals with a number of other well known Late Triassic vertebrate taxa is important. Furthermore, the stratigraphically lower of the two mammalian localities, which on present evidence is Norian in age, represents one of the earliest known occurrences of mammals. Most early mammalian fossils, particularly the best represented forms (*Morganucodontidae*, *Kuehneotheriidae*), are from deposits of either Early Jurassic or Rhaetic age (Clemens 1986). Well substantiated pre-Rhaetic occurrences are few. Fraser, Walkden & Stewart (1985) interpreted the English Emborough fissure deposit containing *Kuehneotherium* teeth to be Norian, but subsequently there has been a lack of consensus on the relative stratigraphical position of this and other mammal-bearing European localities (Buffetaut & Martin 1985; Hahn, Sigogneau-Russell & Wouters 1989). A partial skull from the Tecovas Member of the Dockum Formation has been interpreted by Lucas & Luo (1993) as a primitive mammal principally of the basis of basicranial features; the age of this specimen (late Carnian) may well predate that of most other early mammalian specimens but its phylogenetic relations are not fully known. In contrast, the premolariform teeth from the lower part of the Ørsted Dal Member are unequivocal in their mammalian morphology and in their association with Norian taxa.

Depositional environments and climates

Clemmensen (1980a,b) interpreted the Middle and Late Triassic sediments of the Jameson Land Basin as principally lacustrine, or occasionally lagoonal, deposits (Fig. 2). The Fleming Fjord Formation, which is very well exposed along the western side of Carlsberg Fjord and in Bjergkronerne, was restudied during the 1991 and 1992 field seasons.

At Tait Bjerg along Carlsberg Fjord the formation has a thickness of 340 m and is composed of a basal Edderfugledal Member, a middle Malmros Klint Member and an upper Ørsted Dal Member (Clemmensen 1980b; Fig. 2). The Edderfugledal Member is here composed of cyclically bedded dolostones, stromatolites and clastic deposits that presumably formed in an ephemeral lake subject to rare marine flooding. This unit, however, has not yielded any significant finds of tetrapods and was therefore not restudied in detail.

The Malmros Klint Member is composed of cyclically bedded, red-brown mudstones and fine-grained sandstones, and along the western side of Carlsberg Fjord these deposits often form nearly vertical cliffs of ca. 130 m. The member can be divided into a lower sand-rich unit and an upper clay-rich unit (Fig. 2). The member is characterized by a composite cyclicity, and five orders of cycles have been recognized at Tait Bjerg. The thickest are the first-order cycles which are approximately 25 m thick. Next in the hierarchy are the second-order cycles which are between 3.8 and 7 m thick (mean, 5.9 m). These cycles are clearly visible in the landscape as major, step-like ledges. The basal part of each cycle is relatively rich in siltstones, whereas the upper part of the cycle is dominated by sandstones. The top of the cycle is defined by a well developed paleosol. These paleosol horizons are enriched in calcite or dolomite (yellowish color) and always possess well developed desiccation cracks (up to 1 m deep in several places). Underlying sandstones are typically bioturbated, and locally contain calcite nodules. On top of the paleosols, well developed, flat-pebble conglomerates occur. These flat-pebble conglomerates are composed of intraformational mud clasts and have thicknesses between a few centimetres and 0.5 m; they frequently contain vertebrate fragments.

All second-order cycles contain thinner cycles. Third-order cycles vary in thickness between 1.25 and 2.2 m with a mean of 1.57 m. These cycles also possess a basal, relatively silt-rich horizon and an uppermost, sandy layer, topped by a paleosol with desiccation cracks and a flat-pebble conglomerate (Fig. 16). These cycles are likewise detectable on the landscape with the uppermost sandy portion forming more resistant ledges. In well exposed sections it is sometimes possible to observe that the third-order cycles are also composite. These minor cycles are primarily defined by a rhythmic distribution of relatively thin (and immature) paleosols. From preliminary data on the stratigraphic distribution of these paleosols, it appears that two orders of minor cycles occur. Fourth-order cycles have a mean thickness of about 0.6m, whereas fifth-order cycles have a mean thickness of 0.25 m.

The composition of the cycles records systematic fluctuations in depositional conditions (Clemmensen 1980a). The lowermost, silt-rich portion of the cycles apparently formed in a large, ephemeral lake or playa-mudflat system during periods of little sand yield to the basin in a relatively humid climate. Thin beds of loess deposits indicate seasonal aridity. The uppermost, sand-rich portion of the cycles formed in an ephemeral lake system with intermittent wave reworking of the sand flats, indicative of a dry climate with seasonal rainfall, and with greater sand transport into the basin. The well developed paleosols clearly indicate periods of exposure and non-sedimentation in an arid climate, whereas the overlying flat-pebble conglomerates indicate flushing of the exposed surfaces by flood or basin water under conditions of increased humidity.

The composite nature of the sedimentary cycles, their rhythmicity, and their thickness ratios are evidence that fluctuations in depositional conditions were controlled by orbitally forced climatic changes (Milankovitch cycles; cf. Olsen 1986). At present, however, it is difficult to

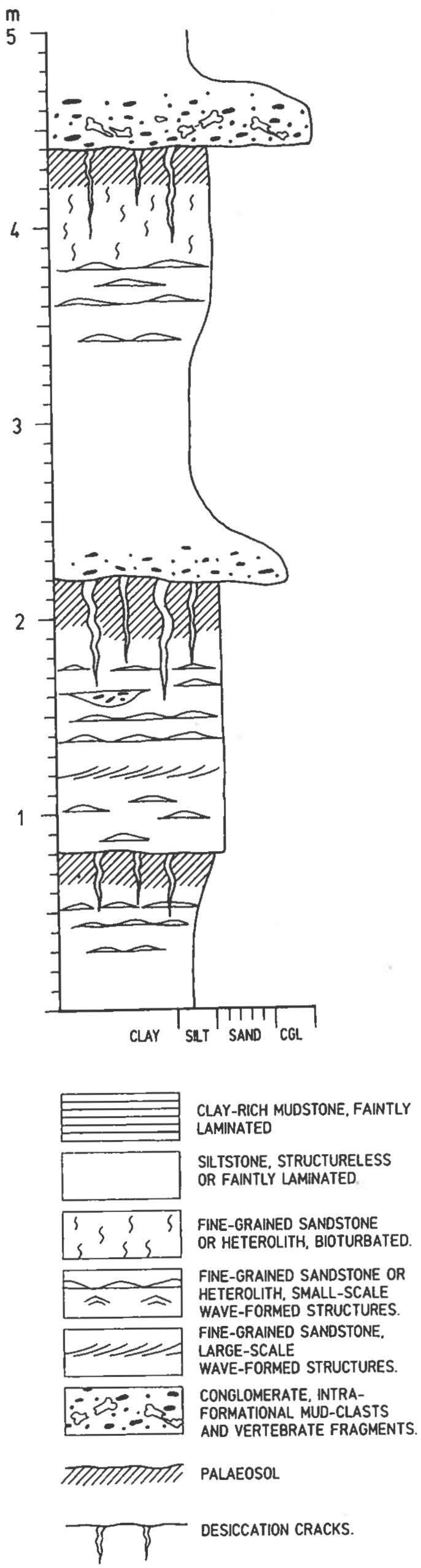


Fig. 16. Sedimentary log of a typical facies in the lower Malmros Klint Member, western slope of Tait Bjerg, showing a sequence of third order depositional cycles.

Table 1. Estimates of the depositional duration of the tetrapod-bearing Malmros Klint Member and Carlsberg Fjord beds (informal name), Fleming Fjord Formation, East Greenland.

Stratigraphic unit	Thickness at Tait Bjerg	Accumulation time	
Carlsberg Fjord beds	115 m	11 m.y.[1]	2.4–3.1 m.y.[2]
Malmros Klint Mb	130 m	9 m.y.[1]	2.1–2.7 m.y.[2]

[1]Assuming that the 4.50 m or 5.89 m cycles are long eccentricity cycles (413,000 yr).

[2]Assuming that the 4.50 m or 5.89 m cycles are short eccentricity cycles (95–123,000 yr).

calibrate the cycles. The prominent second-order cycles could be either short (95–123,000 yr) or long (413,000 yr) eccentricity cycles. Thus the Malmros Klint Member could have accumulated over about 2.4 million years or over about 9 million years (Table 1). Deposition was clearly not continuous, as indicated by the numerous paleosol horizons; the times of accumulation suggested here include both depositional time and periods of subaerial exposure and soil formation.

The Ørsted Dal Member in the region between Carlsberg Fjord and Fleming Fjord is composed of a basal clastic unit, here informally termed the Carlsberg Fjord beds, and an overlying unit of mixed clastics and carbonates termed the Tait Bjerg Beds (Fig. 2). The Carlsberg Fjord beds are about 115 m thick and are composed of cyclic, bedded claystones or silty claystones and thin sandstones (Fig. 17). This unit is also characterized by a well-developed composite cyclicity. At Tait Bjerg the thickest cycles are about 4.5 m, intermediate cycles are 1.5 m thick, and minor cycles are about 0.3 m thick. The dominant facies in the cycles is red or violet claystone, or silty claystone with horizontal lamination. Commonly violet claystones are overlain by more silty, redbrown claystones. These claystones contain sandstone laminae, thin paleosols, and some intraformational conglomerates with bone fragments (Fig. 17); occasionally more complete vertebrate remains are found in these deposits. The sandstones (2–5 cm thick), which represent the top of the cycles, weather to a grayish or greenish color; they are characterized by small-scale, wave-formed or current-formed cross lamination and more rarely large-scale, current-formed cross lamination. Upper bedding planes frequently contain desiccation features, wave ripple marks, and dinosaur tracks. Sole surfaces contain abundant fresh-water trace fossils (Bromley & Asgaard 1979). Native copper occurs in two relatively thick sandstones at the base of the unit (Thomassen *et al.* 1982). Wave ripples in the sandstones trend dominantly ESE-WNW with a subordinate number trending NE-SW (see also Clemmensen 1980a). These data indicate deposition in a shallow or ephemeral lake influenced by predominant winds from the NNE. Apparently the center of the lake was situated NW of the study area in the region of modern day Fleming Fjord.

The cyclic pattern of the Carlsberg Fjord beds is evidence that depositional conditions in the basin continued to be controlled by Milankovitch-type fluctuations in climate (*sensu* Olsen 1986). Thus, the violet claystones probably formed in a subaqueous environment during periods of relatively high water level in the basin with a humid climate, whereas the redbrown claystones may indicate deposition during a lower water level in the basin with a more arid climate. The sandstones primarily seem to represent lacustrine sand flat deposits and probably formed during periods of increased run-off to the basin

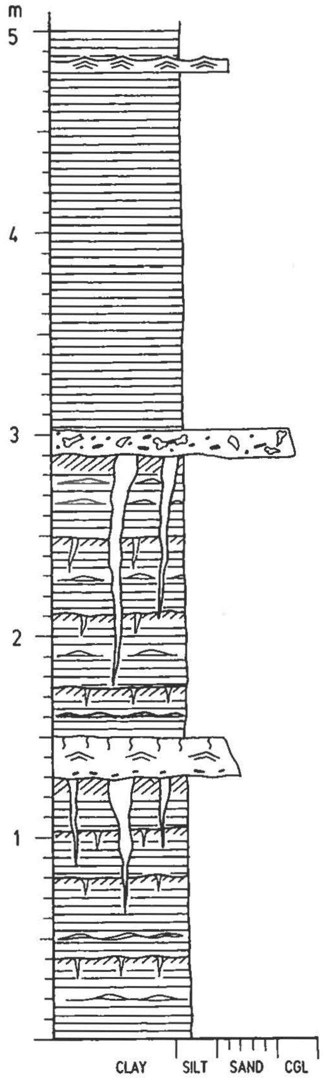


Fig. 17. Sedimentary log of a bone bed and associated deposits in the lowermost part of the Ørsted Dal Member (Carlsberg Fjord beds), western slope of Tait Bjerg. The bone bed yielded two mammalian premolariform teeth (MCZ Field No. 62/91G No. 1, No. 2) as well as theropod, prosauropod and ?phytosaur teeth, amphibian dermal armor, coprolites and fish remains.

during a transition from an arid to a humid climate. From data on cycle thickness it may be estimated that the Carlsberg Fjord beds accumulated either over a period of about 2.8 million years, or over a period of about 11 million years (Table 1).

The carbonate-bearing Tait Bjerg Beds were only briefly examined during the 1991 and 1992 sedimentological studies along Carlsberg Fjord. The beds are composed of cyclically bedded, dark, clastic mudstones and lightgrey or yellowish, impure limestones or dolomitic limestones and clastic sandstones. The unit has a thickness of 50–60 m along the western side of Carlsberg Fjord. Preliminary data on this unit indicate composite cyclicity with prominent cycles having a thickness of about 5 m. Dinosaur tracks were observed on several bedding planes. The cyclicity of the Tait Bjerg Beds records their formation during regular, climatically related variations in lake level. Periodic marine flooding of the basin throughout this time interval was suggested by Clemmensen (1980a,b). No unequivocally marine macrofossils were found in the Tait Bjerg Beds; a more definitive conclusion on the salinity of the basin water must await the results of micropaleontological analyses.

At Gipsdalen, 50 km NW of Tait Bjerg, the Fleming Fjord Formation is likewise composed of a basal Edderfugledal Member (40 m thick), a middle Malmros Klint Member (60 m thick) and an uppermost Ørsted Dal Member (180 m thick) (Fig. 2). The cliff-forming, sand-rich lower unit of the Malmros Klint Member is much thinner here, whereas the upper, clay-rich unit of the Malmros Klint Member has increased in thickness, probably indicating that this part of the basin was close to the lake center during deposition of the Malmros Klint Member. The overlying Ørsted Dal Member is here composed of a basal, relatively coarse-grained siliciclastic unit, the Bjergkronerne beds, and an overlying, thin and poorly exposed, carbonate-rich unit, the Tait Bjerg Beds. The Bjergkronerne beds are about 170 m thick and composed of cyclically interbedded fluvial or delta distributary channel sandstones (light grey) and clay-rich lacustrine deposits (red or variegated). The most prominent cycles have a thickness of about 7 m and probably reflect climatically controlled fluctuations in precipitation and fluvial discharge. Paleocurrent data indicate that fluvial discharge was towards the E and SE. The Bjergkronerne Beds display an overall coarsening upward trend in grain size that indicates that the fluvial system was prograding probably in relation to a long-term climatic change.

Conclusions

The Late Triassic Fleming Fjord Formation preserves a diverse vertebrate fauna now known to include mammals, reptiles (prosauropod and theropod dinosaurs, turtles, pterosaurs and aetosaurs), amphibians (plagiosaurids, capitosaurs) and fishes (including lungfish, coelacanths, actinopterygians and sharks). Initial identifications of fossil tetrapod taxa support the interpretation that the fauna is predominantly European in aspect and that the upper part of the formation, principally the Ørsted Dal Member, is of Norian age. The cyclicity of depositional conditions, and the inferred climatic fluctuations, are consistent with the diversity of the faunal representation which ranges from both small and large sized terrestrial animals to abundant amphibians and obligatorily aquatic forms.

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This report covers four field seasons. The initial survey, 1 July – 1 August 1988, was undertaken by Farish A. Jenkins, Jr., William W. Amaral, Charles R. Schaff (all of Harvard University) and Neil H. Shubin (University of California, Berkeley). The second field season, 30 June – 4 August 1989, was staffed by FAJJr., WWA, Stephen M. Gatesy (all of Harvard University), NHS (University of Pennsylvania) and H. Edgar Jenkins II (San Anselmo, California). For the third field season, 10 July – 18 August 1991, participants were FAJJr, WWA, SMG, HEJII, CRS, NHS; Niels Bonde, Lars B. Clemmensen and Frank Osbæck (University of Copenhagen); James F. Dice, Jr., (Tufts University) and William R. Downs (Northern Arizona University). Participants in the fourth field season, 25 June – August 4 1992, were FAJJr, WWA, LBC, WRD, SMG, CRS, NHS, Amy R. Davidson (Harvard University) and Dennis V. Kent (Columbia University).

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Meddelelser om Grønland, GEOSCIENCE

A "deep" ice core from East Greenland

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Johnsen, S. J., Clausen, H. B., Dansgaard, W., Gundestrup, N. S., Hansson, M., Jonsson, P., Steffensen, J. P. & Sveinbjørnsdottir, A. E. 1992. A "deep" ice core from East Greenland. Meddr Grønland, Geosci. 29, 22 pp. Copenhagen 1992-11-24.

Pilot studies on the Renland peninsula in Scoresbysund Fjord, East Greenland, indicated that the relatively small and separate Renland ice cap meets most of the criteria defining a favourable ice-core drill-site. In 1988, a Nordic expedition recovered a continuous surface-to-bedrock ice core from the summit. This relatively short core reaches deep into the past, probably throughout the last glaciation and through most of the preceding interglacial, Eem, 125,000 years B.P. The core contains detailed information on temporal changes of the coastal environment, and serves as a valuable complement to the new deep ice cores being drilled in Central Greenland. Core analyses suggest that (**1**) during Eemian time the East Greenland climate was at least 5°C warmer than now, and the precipitation 20% higher; (**2**) during the last glacial period, the precipitation decreased to a minimum, perhaps only 20% of the present value; (**3**) the post-glacial climatic optimum was 2.5°C warmer than now; (**4**) the long-term variability of the record is relatively low, due to isostatic movements in the area; and (**5**) from 70,000 years B.P., the Greenland glacial climate alternated between two quasi-stable stages. The latter point may reflect a chaotic feature of climate. If so, climate predictions will be difficult to access.

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Plant and arthropod remains from the palaeo-Eskimo site on Qeqertasussuk, West Greenland

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Samples from the excavation of a palaeo-Eskimo site, settled ca. 3900–3100 ^{14}C yrs BP on a raised beach, were analyzed for pollen and botanical and entomological macro-remains.

In the dwelling area the original vegetation of grasses and *Saxifraga* spp. was covered by thick culture layers; under the midden *Elymus mollis* formed the original vegetation. During short uninhabited periods different grasses dominated. Following the termination of the habitation a mossy heath spread over the area.

The sediments contained abundant well-preserved fragments of insects and other arthropods. Besides oribatid mites, spiders and fly puparia, remains of beetles are predominant. *Micralymma brevilingue* plays a prominent role, but also *Simplocaria metallica*, *Byrrhus fasciatus* and the heteropteron *Nysius groenlandicus* are fairly numerous. A former warm period is indicated by the finds of species at or well north of their present northern limit.

The succession of arthropod assemblages agrees with the palaeobotanical and archaeological evidences. The fauna indicates the transition from typical arctic conditions: few species and low density, to stages with much higher diversity and density following fertilization, but also to stages of inferior conditions for plants and insects as a result of intensive human activity.

A lake pollen diagram shows that after a short pioneer zone first *Salix glauca*, then ca. 6400 ^{14}C yrs BP, *Betula nana* immigrates. Shortly before 3000 BP more cool/humid conditions are indicated in accordance with the general trend in the Holocene climatic development of West Greenland, which is briefly discussed and summarized.

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Report from the Qeqertasussuk Project No. 1.

Key words:
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Acanthostega gunnari, a Devonian tetrapod from Greenland; the snout, palate and ventral parts of the braincase, with a discussion of their significance

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The snout, including the naris and choana, and the palate, ventral parts of the braincase and suspensorium of *Acanthostega gunnari* are described from three-dimensional specimens and sections. The naris is low on the snout, and the choana and vomerine dentition resemble those of osteolepiform fishes. The braincase is ossified in two portions in ventral view, with the ventral cranial fissure still evident. Dorsally, however, the otic region and sphenethmoid are co-ossified, so there was no movement possible between them. The palate is "closed" as in osteolepiforms and primitive tetrapods, and the parasphenoid is grooved as in some osteolepiforms. It is argued that the low naris and divided braincase represent the primitive condition for tetrapods, and that the condition of the naris and choana most closely resemble those of panderichthyiid fishes among sarcopterygians.

Key words:
Devonian, tetrapod, *Acanthostega*, snout, palate, braincase, choana, naris.

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