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The Late Triassic vertebrate fauna of the Jameson Land Basin, East Greenland: description, phylogeny, and paleoenvironmental implications

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2019

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Tudo em nós está em nosso conceito do mundo;
modificar o nosso conceito do mundo é modificar o mundo para nós,
isto é, é modificar o mundo,
pois ele nunca será, para nós, senão o que é para nós.
Fernando Pessoa – Livro do Desassossego

Di quei tempi ero fatto per sprofondare,
ad ogni parola che mi fosse detta, o mosca che vedessi volare,
in abissi di riflessioni e considerazioni che mi scavavano dentro e bucheravano giù per torto
e su per traverso lo spirito, come una tana di talpa;
senza che di fuori ne paresse nulla.
Luigi Pirandello – Uno, Nessuno e Centomila

Nothing really matters, anyone can see
Nothing really matters
Nothing really matters to me
Anyway the wind blows
Queen – Bohemian Rhapsody

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RESUMO

As rochas do Triásico Superior que afloram na Bacia de Jameson Land (Leste da Gronelândia) e constituem a Formação do Fleming Fjord, são ricas em fósseis de vertebrados, registando todos os principais grupos de vertebrados conhecidos da época, incluindo algumas espécies únicas.

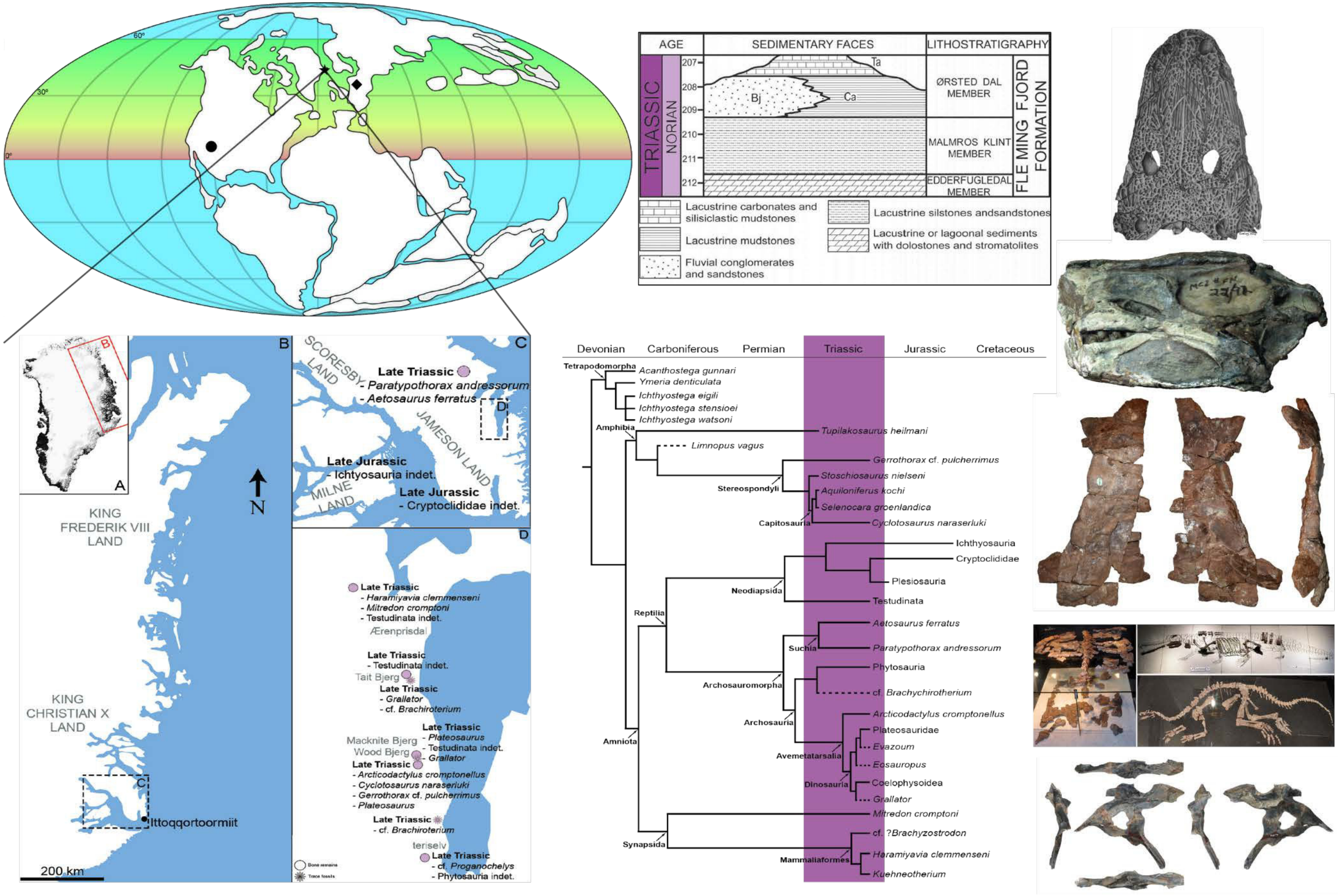
Esta tese de doutoramento, tem como base os resultados fósseis das expedições EUA-Dinamarca ao leste da Gronelândia durante o final dos anos 80, década de 1990, início da década de 2000 e as novas expedições que participámos de 2012 a 2016. A estrutura principal desta tese segue a ordem filogenética da fauna de vertebrados do Triásico Superior da Gronelândia, fornecendo a mais completa actualizada síntese dos tetrápodes fósseis paleozóicos e mesozóicos conhecidos da Gronelândia, com um registo fotográfico único de todos os holótipos gronelandeses, incluindo alguns dos fósseis mais emblemáticos da paleontologia (Capítulo 1). O registo fóssil de tetrápodes do Paleozóico e Mesozóico da Gronelândia inclui, pelo menos, 30 táxones. Uma secção final incluindo novos dados sobre restos de fitossauros e sauropodomorfos foi adicionada ao artigo original.

Descobertas durante as expedições de 2012 e 2016 permitiram a descrição de um novo peixe pulmonado Ceratodus tunuensis (Dipnoi: Ceratodontidae).

O capítulo 3 é o fornece um dos artigos publicados que compõem esta tese. Trata-se da descrição de uma nova espécie de anfíbio ciclotossauro, Cyclotosaurus naraserluki (Temnospondyli: Capitosauroidea), um predador de água doce semelhante a uma salamandra com um crânio de mais de meio metro de comprimento. Os Capítulos 4–6, inéditos, incluem a descrição de três novas espécies do Triásico Superior de Flemming Fjord: um aetossauro Stagonolepididae, um Testudinata basal e um dinossauro terópode basal.

O capítulo 7 conclui esta tese, avaliando as implicações paleoecológicas, paleogeográficas, paleoambientais e paleoclimáticas do cortejo faunístico do Fleming Fjord em comparação com faunas coevas da Europa e América do Norte, ligando a fauna de vertebrados da Gronelândia intimamente relacionada com a Europa do que a América do Norte.

Palavras-chave: Tardo Triássico, Gronelândia, Formação do Fleming Fjord, Vertebrata, paleogeografia, paleoclima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- Aetosaurus ferratus
D
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MILNE LAND
Late Jurassic
- Cryptoclididae indet.
Late Triassic
- Haramiyavia clemmenseni
- Mitredon cromptoni
- Testudinata indet.
Ærenprisdal
Late Triassic
- Testudinata indet.
Tait Bjerg
Late Triassic
- Grallator
- cf. Brachiroterium
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- Plateosaurus
- Testudinata indet.
- Grallator
Macknite Bjerg
Wood Bjerg
Late Triassic
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MALMROS KLINT MEMBER
EDDERFUGLEDAL MEMBER
FLE MING FJORD FORMATION
Lacustrine carbonates and silisiclastic mudstones
Lacustrine mudstones
Fluvial conglomerates and sandstones
Lacustrine silstones andsandstones
Lacustrine or lagoonal sediments with dolostones and stromatolites
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Tetrapodomorpha
Acanthostega gunnari
Ymeria denticulata
Ichthyostega eigili
Ichthyostega stensioei
Ichthyostega watsoni
Amphibia
Tupilakosaurus heilmani
Limnopus vagus
Gerrothorax cf. pulcherrimus
Stereospondyli
Stoschiosaurus nielseni
Aquiloniferus kochi
Selenocara groenlandica
Capitosauria
Cyclotosaurus naraserluki
Ichthyosauria
Cryptoclididae
Plesiosauria
Neodiapsida
Testudinata
Reptilia
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cf. ?Brachyzostrodon
Synapsida
Mammaliaformes
Haramiyavia clemmenseni
Kuehneotherium

ABSTRACT

The Late Triassic rocks cropping out at the Jameson Land Basin (East Greenland) forming the Fleming Fjord Formation are rich in vertebrate fossils, recording all the main groups of vertebrates known from the epoch, including some unique species.

This PhD project, standing on the fossils findings by of the US-Danish expeditions to East Greenland during the late 1980's, 1990's, early 2000's, and the new expeditions that we participated from 2012 to 2016.

The main structure of this thesis follows the phylogenetic order of the Late Triassic vertebrate fauna from Greenland, providing the most complete to-date synthesis on the known Paleozoic and Mesozoic fossil tetrapods of Greenland, with a unique photographical record of all the Greenlandic holotypes, including some of the most iconic fossils for paleontology (Chapter 1). The tetrapod fossil record of the Paleozoic and Mesozoic of Greenland includes, at least, 30 taxa. A final section including new data on phytosaur and sauropodomorph remains has been added to the original article.

Discoveries during the 2012 and 2016 expeditions allowed the description of a new lungfish *Ceratodus tunuensis* (Dipnoi: Ceratodontidae).

Chapter 3 is the last up-to-date of the published papers that compose this thesis. It is about the description of a new species of cyclotosaur amphibian, *Cyclotosaurus naraserluki* (Temnospondyli: Capitosauroidea), a salamander-like freshwater predator with a skull over half a meter long.

The yet unpublished Chapters 4–6 includes the description of three new species from the Late Triassic of the Flemming Fjord Fm.: a Stagonolepididae aetosaur, a basal Testudinata, and a basal theropod dinosaur.

Chapter 7 concludes this thesis, assessing the paleoecological, paleogeographic, paleoenvironmental, and paleoclimate implications of the Fleming Fjord faunal assemblage in comparison with coeval faunas from Europe and North America, linking the vertebrate fauna of Greenland closely related to Europe than North America.

Keywords: Late Triassic, Greenland, Fleming Fjord Formation, Vertebrata, paleogeography, paleoclimate

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Figure 1.12 - The tupilakosaurid *Tupilakosaurus heilmani* Nielsen 1954, holotype MGUH VP 3328 (specimen A): two separate blocks containing postcranial material (including vertebrae, ribs, tooth) from the Early Triassic of the Wordie Creek Group. A: Block A. B: Block B. Scale bars: 5 cm.

Figure 1.13 - Fossil tetrapods from the Late Triassic of Jameson Land Basin in exhibition at the GeoCenter of Møns Klint, Denmark, as of 2016. A: Oblique photograph of the holotype of the capitosaurid *Cyclotosaurus naraserluki* Marzola et al. 2017b MGUH.VP 9522. B: The stagonolepidid *Aetosaurus ferratus* Fraas 1877 NHMD 190375–190379 (previously MCZ Field no. 22/92G). C: Oblique photograph of the Testudinata NHMD 190349 (previously MCZ Field no. 22/88G) (top layer: carapace; bottom layer: plastron and limb bones). D: Adult and juvenile (bottom right corner) phytosaurs, respectively NHMD 74733 and NHMD 74736. E: Sauropodomorph

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Figure 1.15 - The cynodont *Mitredon cromptoni* Shapiro & Jenkins 2001, holotype MGUH VP 3392: a left dentary from the Late Triassic of the Fleming Fjord Formation. A: lingual view. B: labial view. Scale bar: 1 cm.

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Figure 1.17 - Early Jurassic plesiosaur from the Kap Stewart Formation of the Jameson land Basin: two vertebrae NHMD 74795 (A–D), NHMD 74756 (E–F) and a rib NHMD 74797 (G–H). A: Dorsal view. B, E, G: Frontal views. C: Lateral right view. D: Lateral left view; F: Ventral view; H: Medial view. Scale bar: 2 cm.

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Figure 2.1 - Location map of the East Greenland showing the Mesozoic deposits in the Jameson Land Basin. A, small insert showing Greenland, with East Greenland indicated by the box. B, geological map of East Greenland, with the Carlsberg Fjord locality indicated by the box. C, close-up of the eastern part of the basin near Carlsberg Fjord and the locality with Upper Triassic rocks at Lepidopteriselv. Modified from Stemmerik et al. (1997).

Figure 2.2 - A, stratigraphic scheme of the Triassic succession exposed at Carlsberg Fjord. B, field photo showing the reddish-brown bedded lacustrine sediments of the Ørsted Dal Member.

Figure 2.3 - *Ceratodus tunuensis*, sp. nov., holotype and referred material. A, E, holotype NHMD 115910, a right upper tooth plate (A), with details of the tooth plate occlusal surface (E); B, NHMD 115911, an upper left tooth plate; C, NHMD 115912, an upper left tooth plate; D, NHMD 115913, fragmentary left lower tooth plate. Abbreviations: cd, circumdenteonal dentine; id, interdenteonal dentine. Scale bar equals 1 cm.

Figure 2.4 - *Ceratodus tunuensis*, sp. nov., referred material. A, NHMD 115914, an incomplete left lower tooth plate; B, NHMD 115915, an incomplete left lower tooth plate; C, D, NHMD 115916, an incomplete left lower tooth plate (C), with details of tooth plate occlusal surface (D). Abbreviations: cd, circumdenteonal dentine; id, interdenteonal dentine. Scale bar equals 1 cm.

Figure 2.5 - *Ceratodus tunuensis*, sp. nov., referred material, NHMD 115917, right lower jaw bone. A, lateral and B, medial views. Abbreviations: pg, prearticular groove; r, Ruge’s ridge; sy, symphysis of jaw bone; tps, tooth plate scar; 5r, fifth ridge. Scale bar equals 2 cm.

Figure 3.1. - A, geographical map of Greenland; B, close-up of Jameson Land and the Liverpool Land area; C, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al. 1998). Stars in B and C indicate the site where the holotype of *Cyclotosaurus naraserluki* was discovered. Abbreviations: Bj, Bjergkronerne beds; Ca, Carlsberg Fjord beds; Ta, Tait Bjerg Beds. Scale bar equals 40 km (B).

Figure 3.2 - The holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522. A, C, photograph and interpretative drawing of dorsal view; B, D, photograph and interpretative drawing of ventral view. Abbreviations: AF, adductor fossa; APV, anterior palatal vacuity; CH, choana; ex, exoccipital; ept, ectopterygoid; f, frontal; ij, insula jugalis; IOS, infraorbital sulcus; j, jugal; l, lacrimal; m, maxilla; n, nasal; NA, naris; OF, otic fenestra; OR, orbit; p, parietal; pal, palatine; pas, parasphenoid; pat, palatine tusk; PF, parietal foramen; PMF, premaxillary foramen; pm, premaxilla; pof, postfrontal; POS, postorbital sulcus; po, postorbital; pp, postparietal; PQF, paraquadrate foramen; prf, prefrontal; ps, parasphenoid; pt, pterygoid; PV, palatal vacuity; q, quadrate; qj, quadratojugal; s, squamosal; st, supratemporal; SOS, supraorbital sulcus; t, tabular; to, tooth; v, vomer; vt, vomerine tusk. Scale bar equals 20 cm.

Figure 3.3 - Artwork of the dorsal view of the holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522, by Ana Luz (Museu da Lourinhã).

Figure 3.4 - Close-up views of the premaxillary foramina (highlighted by white arrows) in cyclotosaurids. A, B, dorsal and ventral views of the holotype of *Cyclotosaurus naraserluki*, MGUH.VP 9522; C, holotype of *Cyclotosaurus mordax*, SMNS 13014. Scale bar equals 5 cm.

Figure 3.5 - The holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522. A, B, photograph and interpretative drawing of right lateral view; C, D, photograph and interpretative drawing of left lateral view; E, F, photograph and interpretative drawing of occipital view. Abbreviations: ex, exoccipital; IOS, infraorbital sulcus; j, jugal; m, maxilla; pm, premaxilla; POS, postorbital sulcus; pp, postparietal; PQF, paraquadrate foramen; pt, pterygoid; sq, squamosal; q, quadrate; qj, quadratojugal; t, tabular. Scale bar equals 20 cm.

Figure 3.6 - MGUH.VP 9523 (A–F) and MGUH.VP 9524 (G–L), vertebral intercentra associated with *Cyclotosaurus naraserluki*. A, G, anterior view; B, H, posterior view; C, I, right lateral view; D, J, left lateral view; E, K, dorsal view; F, L, ventral view. The visible labels on specimens refer to a former labeling system. Scale bars equal 2 cm.

Figure 3.7 - Most parsimonious tree of the Capitosauroidea (sensu Schoch 2008) produced by a TNT 1.5 analysis (tree length D 109 steps, consistency index D 0.624, retention index D 0.680, rescaled consistency index D 0.424). Synapomorphies are shown along the tree and numbers refer to the characters listed in the phylogeny in Witzmann et al. (2016). Thicker branches represent the genus *Cyclotosaurus* in the analysis. Abbreviations: C., *Cyclotosaurus*; R, reversal.

Figure 3.8 - Most parsimonious tree presented in Figure 7 showing Bremer support values (number over the branches) >1 and bootstrap values (numbers under the branches) after 1000 replicates.

Figure 4.1 - A, geographical map of the Jameson Land area of East Greenland; B, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al. 1998). Stars indicate the locality and the stratigraphic position of the aetosaur remains. Abbreviations: Bj, Bjergkronerne beds; Ca, Carlsberg Fjord beds; Ta, Tait Bjerg Beds.

Figure 4.2 - *Sikuqisik jenkinsi* gen. et sp. nov.: skull NHMD 190376. A, lateral left; B, lateral right; C, dorsal; D, ventral; E, frontal; and F, posterior orthogonal views obtained by the photogrammetric model.

Figure 4.3 - *Sikuqisik jenkinsi* gen. et sp. nov.: skull NHMD 190376. A, lateral left; B, lateral right; C, dorsal; D, ventral; E, frontal; and F, posterior orthogonal views obtained by the photogrammetric model ventral orthogonal views in solid color, obtained by the photogrammetric model. The arrow in E shows the perspective from which the drawing in Fig. 4 was taken. Abbreviations: a, articular; AOF, antorbital fenestra; d, dentary; dt, dentary tooth; f, frontal; hy, hyoid; ITF, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; MAF, mandibular fenestra; mt, maxillary tooth; n, nasal; OR, orbit; p, parietal; pa, palatine; po, postorbital; pof, postfrontal; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; QF, quadrate foramen; qj, quadratojugal; s, squamosal; sa, surangular; sp, splenial; STF, supratemporal fenestra.

Figure 4.4 - *Sikuqisik jenkinsi* gen. et sp. nov.: an interpretative drawing of the left side from perspective perpendicular to the side plane (see arrow in Fig. 3E). Abbreviations: a, articular; AOF, antorbital fenestra; d, dentary; dt, dentary tooth; f, frontal; ITF, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; MAF, mandibular fenestra; mt, maxillary tooth; n, nasal; OR, orbit; p, parietal; pof, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; s, squamosal; sa, surangular; sp, splenial; STF, supratemporal fenestra

Figure 4.5 - *Sikuqisik jenkinsi* gen. et sp. nov.: sequence of the four dorsal vertebrae in anatomical connection, NHMD 190379. A, dorsal; B, lateral right; C, ventral; D, anterior; and E, posterior orthogonal views. Abbreviations: di, diapophysis; nc, neural canal; par, parapophysis; podl, postzygadiapophyseal lamina; prpl, prezygaparapophyseal lamina; spol, spinopostzygapophysea lamina.

Figure 4.6 - *Sikuqisik jenkinsi* gen. et sp. nov.. A, block NHMD 190378 containing dorsal osteoderms and a left femur. B, close-up of the left femur; C–F, close-ups of four dermal osteoderms; G, natural imprint of the dorsal surface of the dorsal osteoderm NHMD 190375.

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Figure 4.8 - Phylogenetic analysis. A, strict consensus tree of nine MPTs from the initial matrix produced by a TNT 1.5 analysis (29 taxa, 83 characters: TL of 203; CI of 0.552; RI of 0.730; RC of 0.403). B, reduced strict

consensus of one parsimonious tree after a priori pruning of *Aetobarbakinoides brasiliensis* (28 taxa, 83 characters: TL of 208; CI of 0.558; RI of 0.736; RC of 0.410). Bremer support values higher than 1 (number over the branches) and bootstrap values after 1000 replicates higher than 50% (numbers under the branches) are shown. C, simplified reduced strict consensus tree (b). Full synapomorphies of non-paratypothoracini Aetosaruinae are shown along the branches and numbers refer to the characters listed in Parker (2016).

Figure 5.1. - A, geographical map of Greenland; B, close-up of Jameson Land and the Liverpool Land area; C, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al. 1998). Stars in B and C indicate the site where the holotype of NHMD Testudinata n. gen. et sp. was discovered. Abbreviations: Bj, Bjergkronerne beds; Ca, Carlsberg Fjord beds; Ta, Tait Bjerg Beds. Scale bar equals 40 km (B).

Figure 5.2 – *NHMD Testudinata gen. et sp. nov.* holotype. Carapace fragment NHMD 163409 E. A, dorsal; B, ventral. Scale bar equals 5 cm.

Figure 5.3 - NHMD Testudinata n. gen. et sp. holotype. Carapace, peripherals. A, NHMD 163398 A; B, NHMD 163398 B; C, NHMD 163398 C. Subscripts: 1, dorsal view; 2, ventral view. Scale bar equals 5 cm.

Figure 5.4 - NHMD Testudinata n. gen. et sp. holotype. Carapace, vertebrals. A, NHMD 163415 C; B, NHMD 163400 C; C, NHMD 163400 A; D, NHMD 163400 B; E, NHMD 163413 C; F, NHMD 163411 E; G, NHMD 163411 H; H, NHMD 163411 F; I, NHMD 163411 I. Subscripts: 1, dorsal view; 2, ventral view; 3, lateral; 4, frontal. Abbreviations: r, rib. Scale bar equals 5 cm.

Figure 5.5 - NHMD Testudinata n. gen. et sp. holotype. Carapace, pleurals. A, NHMD 163415 A; B, NHMD 163400 D-E; C, NHMD 163392 E; D, NHMD 163417 B; E, NHMD 163391 J; F, NHMD 163413 B; G, NHMD 163413 L; H, NHMD 163413 A; I, NHMD 163411 B; J, NHMD 163411 A; K, NHMD 163411 G. Subscripts: 1, dorsal view; 2, ventral view; 3, lateral; 4, frontal. Light yellow parts were reconstructed during preparation. Abbreviations: r, rib. Scale bar equals 10 cm.

Figure 5.6 - NHMD Testudinata n. gen. et sp. holotype. Carapace, costals. A, NHMD 163415 C; B, NHMD 163392 A; C, NHMD 163392 D; D, NHMD 163404 B; E, NHMD 163417 A; F, NHMD 163413 D; G, NHMD 163413 E. Subscripts: 1, dorsal view; 2, ventral view. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.7 - NHMD Testudinata n. gen. et sp. holotype. Plastron element NHMD 163409 F in A, dorsal; B, ventral; and C, lateral views. Scale bar equals 10 cm.

Figure 5.8 - NHMD Testudinata n. gen. et sp. holotype. Plastron elements. A, NHMD 163409 B; B, NHMD 163409 D; C, NHMD 60 C; D, NHMD 60 A; E, NHMD 60 E. Subscripts: 1, dorsal view; 2, ventral view; 3, lateral. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.9 - NHMD Testudinata n. gen. et sp. holotype. Left scapulacoracoid NHMD 163389 in A, lateral; B, medial; C, anterior; D, posterior; E, ventral; and F, dorsal views. Abbreviations: co, coracoid; dp, dorsal process; g, glenoid. Light yellow parts were reconstructed during preparation. Scale bar equals 10 cm.

Figure 5.10 - NHMD Testudinata n. gen. et sp. holotype. Right scapulacoracoid NHMD 163390 in A, lateral; B, medial; C, dorsal; D, ventral; E, anterior; and F, posterior views. Abbreviations: ap, acromion process; co, coracoid; dp, dorsal process; g, glenoid. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.11 - NHMD Testudinata n. gen. et sp. holotype. Left humerus NHMD 163396 A in A, posterior; B, dorsal; C, ventral; D, anteriro; and E, proximal views. Abbreviations: delt, deltopectoral crest; lat, lateral process; sh, shoulder. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.12 - NHMD Testudinata n. gen. et sp. holotype. Right humerus NHMD 163390 C in A, posterior; B, dorsal; C, ventral; D, anterior; and E, proximal views. Abbreviations: delt, deltopectoral crest; lat, lateral process; med, medial process; sh, shoulder. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.13 - NHMD Testudinata n. gen. et sp. holotype. Left radius NHMD 163389 D in A, lateral; B, ventral; C, dorsal; D, medial; and E, proximal views. Abbreviations: rua, radio-ulnar articulation; rul, radio-ulnar ligament. Scale bar equals 5 cm.

Figure 5.14 - NHMD Testudinata n. gen. et sp. holotype. Left ulna NHMD 163389 C in A, posterior; B, dorsal; C, ventral; D, anteriro; and E, proximal views. Abbreviations: bic, bicipital tendon attachment; ole, olecranon; rua, radio-ulnar articulation; sig, sigmoid notch. Scale bar equals 5 cm.

Figure 5.15 - NHMD Testudinata n. gen. et sp. holotype. Right pelvis NHMD 163406 in A, lateral; B, medial; C, anterior; D, posterior; E, dorsal, and F, ventral views. Abbreviations: ac, acetabulum; aip, anterior ilial process; is, ischium; pip, posterior ilial process. Light yellow parts were reconstructed during preparation. Scale bar equals 10 cm.

Figure 5.16 - NHMD Testudinata n. gen. et sp. holotype. Left pelvis NHMD 163396 B in A, lateral; B, medial; C, posterior; D, anterior; E, dorsal, and F, ventral views. Abbreviations: ac, acetabulum; il, ilium; is, ischium; pu, pubis. Scale bar equals 10 cm.

Figure 5.17 - NHMD Testudinata n. gen. et sp. holotype. Right femur NHMD 163398 A-B in A, posterior; B, dorsal; C, ventral; D, anterior; E, proximal, and F, distal views. Abbreviations: fc, fibular crest; info, intercondylar fossa; pofo, popliteal fossa; tmaj, trochanter major; tmin, trochanter minor. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

Figure 5.18 - NHMD Testudinata n. gen. et sp. holotype. Left femur NHMD 163389 B and 23 D in A, anterior; B, dorsal; C, ventral; D, posterior; E, proximal, and F, distal views. Subscripts: 1, proximal; 2, distal. Abbreviations: info, intercondylar fossa; pofo, popliteal fossa; tic, tibial condyle; tmaj, trochanter major; tmin, trochanter minor. Scale bar equals 5 cm.

Figure 5.19 - NHMD Testudinata n. gen. et sp. holotype. Right tibia NHMD 163393 in A, medial; B, dorsal; C, ventral; D, lateral; E, proximal, and F, distal views. Abbreviations: iol, interosseous ligament; lco, lateral condyle; mco, medial condyle; pco, posterior condyle; tfap, tibial facet for the ascending process of astragalus; tia, tibialis anterior; trf, triceps femoris. Scale bar equals 5 cm.

Figure 5.20 - NHMD Testudinata n. gen. et sp. holotype. Left tibia NHMD 163395 A in A, medial; B, dorsal; C, ventral; D, lateral; and E, proximal views. Abbreviations: cnc, cnemial crest; fcr, fibular crest; iol, interosseous ligament; lco, lateral condyle; mco, medial condyle; pat, patellar tendon attachment; pco, posterior condyle; tia, tibialis anterior. Scale bar equals 5 cm.

Figure 5.21 - Strict consensus tree of sixsteen MPTs of the phylogenetical matrix after Li et al. (2016) produced by a TNT 1.5 analysis (53 taxa, 280 characters: TL is 1207; CI is 0.269; RI is 0.586; RC is 0.158).

Figure 5.22 - Reconstruction of the Late Triassic Greenland Testudinata NHMD 190349. Carapace and caudal vertebrae in A, ventral and B, dorsal views. Scale bar equals 20 cm.

Figure 5.23 - Reconstruction of the Late Triassic Greenland Testudinata NHMD 190349. Plastron in A, dorsal and B, ventral views. Scale bar equals 20 cm.

Figure 5.24 - The Late Triassic Greenland Testudinata NHMD 74737. An imbricated carapace scute in A, dorsal; B, ventral; and C, lateral left views. A'–C' are interpretative drawings of A–C. Scutes in grey are posterior to the ones in white. Scale bar equals 5 cm.

Figure 5.25 - The Late Triassic Greenland Testudinata NHMD 74737. Imbricated carapace scutes in A, dorsal; B, ventral; and C, lateral left views. A'–C' are interpretative drawings of A–C. Scutes in grey are posterior to the ones in white. Scale bar equals 5 cm.

Figure 6.1 - Lithology and track levels at (A) 2016 camp mountain (from Agnolin et al. 2018) and (B) at Track Mountain (Clemmensen, unpublished data). Also indicated the tree main sites with vertebrate remains.

Figure 6.2 - Holotype of *NHMD Theropoda n. gen. et sp.*, NHMD 74732, left pelvis in A, dorsal; B, posterior; C, lateral; D, anterior; E, medial, and; F, ventral views. A'–F' are digital models of NHMD 74732. Abbreviations: ac, acetabulum; il, ilium; is, ischium; ob, obturator foramen; pu, pubis.

Figure 6.3 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195732, left jugal in A, lateral and; B, medial views. Abbreviations: mc, contact with the maxillary; poc, contact with the postorbital; qjc, contact with the quadratojugal.

Figure 6.4 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195727, left scapula in A, lateral; B, frontal; C, medial; D, posterior, and; E, ventral views. A'–E' are digital models of NHMD 195727. Abbreviations: acr, acromion; g, glenoid; sb, scapular blade.

Figure 6.5 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195734, right scapula in A, medial, and; B, lateral views. A'–B' are digital models of NHMD 195734. Abbreviations: acr, acromion; g, glenoid; sb, scapular blade.

Figure 6.6 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195729, right femur in A, anterior; B, medial; C, posterior; D, lateral; E, dorsal, and; F, ventral views. A'–F' are digital models of NHMD 195729. Abbreviations: alt, anterolateral tuber; cflf, caudofemoralis longus fossa; ctf, crista tibiofibularis; fc, fibular condyle; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; lt, lesser trochanter; pofo, popliteal fossa; pmt, posteromedial tuber; tc, tibial condyle; ve, ventral emargination.

Figure 6.7 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195728, right femur in A, anterior; B, medial; C, posterior; D, lateral, and; E, dorsal views. A'–E' are digital models of NHMD 195728. Abbreviations: cflf, caudofemoralis longus fossa; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; lt, lesser trochanter; ve, ventral emargination.

Figure 6.8 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195730, left femur in A, anterior; B, lateral; C, posterior; D, medial, and; E, dorsal views. A'–E' are digital models of NHMD 195730. Abbreviations: cflf, caudofemoralis longus fossa; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; lt, lesser trochanter; ve, ventral emargination.

Figure 6.9 - Referred material to *NHMD Theropoda n. gen. et sp.*, NHMD 195733, right? phalanx in A, anterior; B, dorsal; C, lateral; D, ventral; E, medial, and; F, posterior views. A'–F' are digital models of NHMD 195733.

Figure 6.10 - Phylogenetic relationships after Ezcurra & Martínez (2016) and Ezcurra (2017).

Figure 7.1 - Mounted phytosaur material at GeoCenter Møns Klint such as in August 2017. An adult individual NHMD 74733, comprised of partial upper skull, lower jaw, teeth, partial fore and hindlimbs, partial shoulder and pelvic girdles, vertebrae, ribs, and dermal scutes. The juvenile individual NHMD 74736 (bottom right corner) is represented by an isolated left humerus.

TABLES

Table 2.1 - Measurements (in mm) of selected specimens of *Ceratodus tunuensis*, sp. nov.

Table 7.1 - List of the photogrammetrized phytosaur specimens from Greenland

Table 7.2 - List of the photogrammetrized sauropodomorph specimens from Greenland

Supplementary Material

S3.1 – PDF 3D model of the holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522

S3.2 – OBJ 3D model of the holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522

S4.1 – PDF 3D model of the holotype specimen of *Sikuqisik jenkinsi*, NHMD 190376

S5.1 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: carapace NHMD 163409 E

S5.2 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: plastron NHMD 163409 F

S5.3 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: plastron NHMD 163408

S5.4 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: left scapulacoracoid NHMD 163389 A

S5.5 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: right scapulacoracoid NHMD 163390 A

S5.6 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: right humerus NHMD 163390 C

S5.7 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: right pelvis NHMD 163406

S5.8 – PLY 3D model of the holotype specimen of NHMD Testudinata n. gen. et sp.: proximal right femur NHMD 163398 B

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S5.24 – PLY 3D model of the Late Triassic Testudinata NHMD 74737: left pelvis

S5.25 – PLY 3D model of the Late Triassic Testudinata NHMD 74737: right distal femur and proximal tibia

S6.1 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: left pelvis NHMD 74732

S6.2 – PLY 3D model of the reffered specimen of NHMD Theropoda n. gen. et sp.: left scapula NHMD 195727

S6.3 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: right scapula NHMD 195734

S6.4 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: right femur NHMD 195728

S6.5 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: right femur NHMD 195729

S6.6 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: left femur NHMD 195730

S6.7 – PLY 3D model of the holotype specimen of NHMD Theropoda n. gen. et sp.: right femur NHMD 195731

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S1.2 – PDF 3D model of phytosaur specimen NHMD 74733: left proximal mandible (field nº Hc4)

S1.3 – PDF 3D model of phytosaur specimen NHMD 74735: right distal snout (field nº 126a)

S1.4 – PDF 3D model of phytosaur specimen NHMD 74733: caudal vertebra (field nº 132)

S1.5 – PDF 3D model of phytosaur specimen NHMD 74733: cervical vertebra (field nº Hc112)

S1.6 – PDF 3D model of phytosaur specimen NHMD 74733: left humerus (field nº Fa85)

S1.7 – PDF 3D model of phytosaur specimen NHMD 74733: right humerus (field nº Gc6)

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S1.15 – PDF 3D model of sauropodomorph specimen NHMD 164734: upper skull

S1.16 – PDF 3D model of sauropodomorph specimen NHMD 164734: right proximal mandible

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S1.18 – PDF 3D model of sauropodomorph specimen NHMD 164734: right and left distal mandible

S1.19 – PDF 3D model of sauropodomorph specimen NHMD 164758: upper skull

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S1.21 – PDF 3D model of sauropodomorph specimen NHMD 164734: braincase with atlas and axis

S1.22 – PDF 3D model of sauropodomorph specimen NHMD 164734: cervical 8

S1.23 – PDF 3D model of sauropodomorph specimen NHMD 164734: dorsal vertebrae 1–2

S1.24 – PDF 3D model of sauropodomorph specimen NHMD 164734: sacrum

S1.25 – PDF 3D model of sauropodomorph specimen NHMD 164734: partial tail (nine caudals)

S1.26 – PDF 3D model of sauropodomorph specimen NHMD 164734: left ilium

S1.27 – PDF 3D model of sauropodomorph specimen NHMD 164734: right ilium

S1.28 – PDF 3D model of sauropodomorph specimen NHMD 164734: right pubis

S1.29 – PDF 3D model of sauropodomorph specimen NHMD 164734: left scapulacoracoid

S1.30 – PDF 3D model of sauropodomorph specimen NHMD 164734: distal left humerus

S1.31 – PDF 3D model of sauropodomorph specimen NHMD 164734: proximal left humerus

S1.32 – PDF 3D model of sauropodomorph specimen NHMD 164734: left manus

S1.33 – PDF 3D model of sauropodomorph specimen NHMD 164734: right manus

S1.34 – PDF 3D model of sauropodomorph specimen NHMD 164734: right astragalus

S1.35 – PDF 3D model of sauropodomorph specimen NHMD 164734: right digit II

S1.36 – PDF 3D model of sauropodomorph specimen NHMD 164734: right digits III-IV

S1.37 – PDF 3D model of sauropodomorph specimen NHMD 164734: right femur

S1.38 – PDF 3D model of sauropodomorph specimen NHMD 164734: left metatarsal I

S1.39 – PDF 3D model of sauropodomorph specimen NHMD 164734: right metatarsal V

S1.40 – PDF 3D model of sauropodomorph specimen NHMD 164734: right tibia

S1.41 – PDF 3D model of sauropodomorph specimen NHMD 164734: ungual

ABBREVIATIONS

Institutions

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **GCMK**, GeoCenter Møns Klint, Borre, Denmark; **MB**, Museum für Naturkunde Berlin, Berlin, Germany; **MCZ**, Museum of Comparative Zoology, Harvard University (Massachusetts, USA); **MGUH**, Geological Museum, University of Copenhagen, Copenhagen, Denmark; **NHMD**, Natural History Museum of Denmark, Copenhagen; **NMMNH**, New Mexico Museum of Natural History, Albuquerque, New Mexico, U.S.A.; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Anatomical abbreviations

a, articular; **ac**, acetabulum; **acr**, acromion; **AF**, adductor fossa; **aip**, anterior ilial process; **amb**, M. ambiens insertion; **AOF**, antorbital fenestra; **ap**, acromion process; **APV**, anterior palatal vacuity; **atr**, antitrochanter; **bf**, brevis fossa; **bic**, bicipital tendon attachment; **bs**, brevis shelf; **bt**, brevis tuberosity; **cd**, circumdenteonal dentine; **cflf**, caudofemoralis longus fossa; **CH**, choana; **co**, coracoid; **cnc**, cnemial crest; **d**, dentary; **delt**, deltopectoral crest; **di**, diapophysis; **dp**, dorsal process; **dt**, dentary tooth; **ex**, exoccipital; **ept**, ectopterygoid; **f**, frontal; **fc**, fibular condyle; **fcr**, fibular crest; **fh**, femoral head; **ft**, fourth trochanter; **g**, glenoid; **gt**, greater trochanter; **hy**, hyoid; **id**, interdenteonal dentine; **ij**, insula jugalis; **il**, ilium; **info**, intercondylar fossa; **iol**, interosseous ligament; **IOS**, infraorbital sulcus; **is**, ischium; **ITF**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **lab**, labium; **lat**, lateral process; **lco**, lateral condyle; **lt**, lesser trochanter; **m**, maxilla; **MAF**, mandibular fenestra; **mc**, contact with the maxillary; **mco**, medial condyle; **med**, medial process; **mt**, maxillary tooth; **n**, nasal; **NA**, naris; **nc**, neural canal; **ob**, obturator foramen; **OF**, otic fenestra; **ole**, olecranon; **op**, obturator process; **OR**, orbit; **p**, parietal; **pal**, palatine; **par**, parapophysis; **pas**, parasphenoid; **pat**, palatine tusk; **pco**, posterior condyle; **PF**, parietal foramen; **pg**, prearticular groove; **pip**, posterior ilial process; **PMF**, premaxillary foramen; **pm**, premaxilla; **po**, postorbital; **poc**, contact with the postorbital; **podl**, postzygadiapophyseal lamina; **pof**, postfrontal; **pofo**, popliteal fossa; **POS**, postorbital sulcus; **pp**, postparietal; **PQF**, paraquadrate foramen; **pra**, prearticular; **prf**, prefrontal; **prpl**, prezygaparapophyseal lamina; **ps**, parasphenoid; **pt**, pterygoid; **pat**, patellar tendon attachment; **pu**, pubis; **PV**, palatal vacuity; **pvp**, posteroventral process; **q**, quadrate; **QF**, quadrate foramen; **qj**, quadratojugal; **qjc**, contact with the quadratojugal; **r**, rib; **rr**, Ruge's ridge; **rua**, radio-ulnar articulation; **rul**, radio-ulnar ligament; **s**, squamosal; **sa**, surangular; **sac**, supraacetabular crest; **sb**, scapular blade; **sh**, shoulder; **sig**, sigmoid notch; **SOS**, supraorbital sulcus; **sp**, splenial; **spol**, spinopostzygapophysea lamina; **sr**, sacral rib insertion; **st**, supratemporal; **STF**, supratemporal fenestra **sy**, symphysis of jaw bone; **t**, tabular; **tc**, tibial condyle; **tfap**, tibial facet for the ascending process of astragalus; **tia**, tibialis anterior; **tib**, tibial articulation area; **tic**, tibial condyle; **tmaj**, trochanter major; **tmin**, trochanter minor; **to**, tooth; **tps**, tooth plate scar; **trf**, triceps femoris; **v**, vomer; **vt**, vomerine tusk; **5r**, fifth ridge

Others

Bj, Bjergkronerne beds; **Ca**, Carlsberg Fjord beds; **Ta**, Tait Bjerg Beds.

INTRODUCTION

The Late Triassic (237–201 Ma) was an epoch of major transition in global land ecosystems and witnessed the early diversification of dinosaurs and other key groups of archosaurian reptiles, such as crocodylomorphs and pterosaurs (e.g., Brusatte et al. 2010). These groups dominated terrestrial communities for the next 140 Myr. Late Triassic lake deposits of late Norian–early Rhaetian age (215–205 Ma) known as the Fleming Fjord Formation are very well exposed along the margin of the Jameson Land Basin in East Greenland. During the Late Triassic, the Jameson Land laid at 40° N (like the modern latitude of Portugal) and the Fleming Fjord Formation fossils are the Late Triassic vertebrate remains with the highest paleolatitude currently known from the northern hemisphere (Kent and Clemmensen 1996; Clemmensen et al. 1998, 2016; Kent and Tauxe 2005; Kent et al. 2014).

These lake deposits have been the subject of detailed sedimentological and paleontological studies since the late 1970s, with many vertebrate fossils having been collected by joint US-Danish expeditions (i.e. Clemmensen 1980; Jenkins et al. 1994; Clemmensen et al. 1998, 2016; Milàn et al. 2004; Mateus et al. 2014; Marzola et al. 2017a, b). The vertebrate fauna of the Fleming Fjord Formation recovered during these expeditions shows the presence of all the main vertebrate groups known during the Late Triassic, comprising actinopterigians and sarcopterigians, amphibians, a plethora of reptiles such as turtles, aetosaurs, phytosaurs, pterosaurs, and both sauropodomorph and theropod dinosaurs, and important early mammals (see Jenkins et al. 1994 1997, 2001, 2008; Clemmensen et al. 1998, 2016; Gatesy et al. 1999; Klein et al. 2016; Lallensack et al. 2017).

However, even though many of these taxa are known from very well-preserved and nearly complete material, most of them had not received detailed analyses and publication, leaving dubious and uncertain the accuracy of their provisional taxonomic identification. Amphibian and reptilian taxa known before this doctoral thesis from the Late Triassic of the Jameson Land Basin of East Greenland were the temnospondyl cyclotosaurid *Cyclotosaurus* cf. *posthumus* and plagiosaurid *Gerrothorax pulcherrimus*, the testudinatan cf. *Proganochelys*, the stagonolepids *Aetosaurus ferratus* and *Paratypothorax andressi*, the eudimorphodontid pterosaur *Arcticodactylus cromptonellus*, and the sauropodomorph dinosaur *Plateosaurus engelhardti*, with only *G. pulcherrimus* and *A. cromptonellus* presenting a proper monographical study (Jenkins et al. 1994, 1997, 2001, 2008). Two new expeditions to the Fleming Fjord Formation in 2012 and 2016 recovered some new material, including the first ever reported phytosaurs from Greenland, a third testudinate, and new specimens of sauropodomorph and theropod dinosaurs (Milàn et al. 2012; Marzola et al. 2017a).

Temnospondyls are a group of well-known primitive amphibians, recorded worldwide from the Early Carboniferous to the Early Cretaceous. The Late Triassic of Greenland records two temnospondyl species: *Gerrothorax pulcherrimus* and *Cyclotosaurus* cf. *posthumus* (Jenkins et al. 1994, 2008). With this study, we presented evidences that the cyclotosaur found in the Fleming Fjord

Formation is a new species, *Cyclotosaurus naraserluki*, that it represents one of the largest known amphibians of its epoch, with a skull of over half a meter in length, undoubtedly having been one of the apex predators of the lacustrine waters during the Late Triassic at the Jameson Land Basin (Marzola et al. 2017b; Chapter 3).

Aetosauria were Late Triassic extensively-armored herbivorous archosaurs with an abundant fossil record from every modern continent except Oceania and Antarctica (Parker 2016). Due to highly distinctive body armor characters, their identification to the genus level is frequent. Thus, their abundance, and wide distribution make them excellent index fossils (Lucas & Heckert 1996). Interrelationships among the aetosaurs are not well understood but two clades are properly recognized, with relatively apomorphic armours: the spinose Desmatosuchinae and the wide-bodied Typothoracisinae (Parker 2016). However, Aetosauria phylogeny is still poor, unclear, and under debate, due to lack of decently described material (see Heckert & Lucas 2003) and unclear phylogenetic analyses, some based on osteoderm characters, some others on endoskeletal (non-osteoderm) characters (Parker 2016). The Greenland aetosaur has been attributed to *A. ferratus* by most recent studies (Schoch 2007; Parker 2016); however, our aimed analysis suggests that it might present some unique characters, specific of a new endemic Greenlandic taxon.

Testudinata are some of the most enigmatic vertebrate groups and both their origin and the phylogeny of their earliest representatives is under debate (i.e. Joyce 2007, 2017; Li et al. 2008; Szczygielski & Sulej 2016; Szczygielski 2017). Remarkably, the Late Triassic of Greenland already records the presence of at least three turtle specimens, one briefly described in Jenkins et al. (1994) as cf. *Proganochelys* and two previously unpublished specimens: one recovered during the expedition to Greenland in 2012, the other recovered during the early 1990's and achieved at the NHMD for decades before being re-discovered by I and Octávio Mateus during a visit at the museum in the Summer 2015. Proganochelidae family includes some of the oldest turtles known, recorded from Late Triassic of Germany, and Thailand (Marcelo et al. 2014). Proganochelidae species are just hypothesized as the sister taxon to all other turtles (Gaffney & Meeker 1983) and their phylogenetic affinities with the oldest known turtles (gen. *Odontochelys*), from the Early Norian of China, is still unknown.

Phytosaurs are a group of extinct large archosauriform reptiles, recorded from the Late Triassic Europe, America, Africa, Asia, and from the Early Jurassic of England (see Maisch & Kapitzke 2010; Jones & Butler 2018). Being considered for a long time as the basal-most group of crocodile-line archosaurs, recent studies suggest that phytosaurs are the sister taxon of Archosauria, having been evolved before the split between crocodile- and bird-line archosaurs (Brusatte et al. 2010; Nesbitt 2011). Previously, the material from Greenland had only been briefly reported in Mateus et al. (2014) and still needs a complete study. The first results of our research on the Greenlandic material show the presence of at least four individuals of phytosaurs at different ontological stages (namely, two adults, a sub adult, and a juvenile), all recovered from the "Mateus quarry" discovered by Octávio Mateus in 2012. Theropod dinosaur material has also been recovered from the very same quarry, leading us to interesting paleoecological and causes of death of these top predators during a very short time.

Theropoda represent one of the most successful group of animals ever existed on Earth, ranging from the Mesozoic bipedal carnivorous dinosaurs to modern birds. Theropoda originated during the Late Triassic, covering eventually a worldwide distribution in all of seven the continents (see Sereno 1999; Rauhut 2003; Tykoski and Rowe 2004; Brusatte 2012). The brunching between theropod dinosaurs and modern Aves happened during the Middle Jurassic, making the avian theropods not only the only group of dinosaurs surviving the K-Pg biological crisis, but also one of the most successful group of vertebrates nowadays, with roughly 20.000 modern species worldwide (Padian and Chiappe 1998; Barrowclough et al. 2016). Their presence in Greenland is dominated by tracks and trackways, which are to be found by the thousands and that overcome in numbers the presence of any other tetrapod trackmaker recorded in the Fleming Fjord Formation, including sauropodomorph dinosaurs and non-dinosaurian archosaurs (Gatesy et al. 1999; Milàn et al. 2004; Klein et al. 2016; Lallensack et al. 2017). A few bones have been discovered during the expeditions of 2012 and 2016, enlightening new hypothesis on the success of these group of animals right from the beginning of the evolution, thanks to a high metabolism that allowed them to patrol hundreds of kilometers seeking actively for preys and, eventually, overcoming the other slower archosaurian competitors.

Sauropodomorpha is a clade that includes some of the most diverse, abundant, and successful herbivorous saurischian dinosaurs, generally divided in the moderate in size "prosauropods", or basal sauropodomorpha (up to 6 m in total body length), and the gigantic Sauropoda (over 30 m) (see Sereno 1999; Prieto-Márquez & Norell 2011). The basal Sauropodomorpha are among the earliest and more primitive dinosaurs. Their fossil record spans from the Carnian (Late Triassic) through the Early Jurassic (Galton and Upchurch 2004). Numerous sauropodomorph material has been recovered from Greenland, with one complete adult individual and a rib cage of a second one both in exhibition at GCMK. A third individual represented by a skull had briefly reported in Jenkins et al. (1994) and ascribed to *Plateosaurus engelhardti*. In June 2017, a fourth individual, probably a sub-adult or juvenile, has been recovered from Harvard crates, including a complete skull, vertebrae, limb bones, and a complete hand. Besides having been recorded both as skeletal and trace fossils, sauropodomorph dinosaurs from Greenland have never been thoroughly studied.

The association of several vertebrate taxa in the Fleming Fjord Formation matches that of well-known late Norian faunas from central Europe, but the Greenland material adds significant new information to our understanding of the paleogeographic and paleolatitudinal distribution of Late Triassic faunal provinces. The herpetological and whole vertebrate fauna of Greenland provides support for the inference of a late Norian–early Rhaetian age for the Fleming Fjord Formation. Moreover, Greenland Late Triassic vertebrate fauna presents more affinities with European coeheval faunas rather than North American ones, regardless being closer to the latter in geographical distance.

CHAPTER 1 - A REVIEW OF PALAEOZOIC AND MESOZOIC TETRAPODS FROM GREENLAND

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Abstract

This article presents a synthesis of Palaeozoic and Mesozoic fossil tetrapods from Greenland, including an updated review of the holotypes and a new photographic record of the main specimens. All fossil tetrapods found are from East Greenland, with at least 30 different known taxa: five stem tetrapods (*Acanthostega gunnari*, *Ichthyostega eigili*, *I. stensioi*, *I. watsoni*, and *Ymeria denticulata*) from the Late Devonian of the Aina Dal and Britta Dal Formations; four temnospondyl amphibians (*Aquiloniferus kochi*, *Selenocara groenlandica*, *Stoschiosaurus nielseni*, and *Tupilakosaurus heilmani*) from the Early Triassic of the Wordie Creek Group; two temnospondyls (*Cyclotosaurus naraserluki* and *Gerrothorax* cf. *pulcherrimus*), one testudinatan (cf. *Proganochelys*), two stagonolepids (*Aetosaurus ferratus* and *Paratypothorax andressorum*), the eudimorphodontid *Arcticodactylus*, undetermined archosaurs (phytosaurs and both sauropodomorph and theropod dinosaurs), the cynodont *Mitredon cromptoni*, and three mammals (*Haramiyavia clemmenseni*, *Kuehneotherium*, and cf. ?*Brachyzostrodon*), from the Late Triassic of the Fleming Fjord Formation; one plesiosaur from the Early Jurassic of the Kap Stewart Formation; one plesiosaur and one ichthyosaur from the Late Jurassic of the Kap Leslie Formation, plus a previously unreported Late Jurassic plesiosaur from Kronprins Christian Land. Moreover, fossil tetrapod trackways are known from the Late Carboniferous (morphotype *Limnopus*) of the Mesters Vig Formation and at least four different morphologies (such as the crocodylomorph *Brachychirotherium*, the sauropodomorph *Eosauropus* and *Evazoum*, and the theropodian *Grallator*) associated to archosaurian trackmakers are known from the Late Triassic of the Fleming Fjord Formation. The presence of rich fossiliferous tetrapod sites in East Greenland is linked to the presence of well-exposed continental and shallow marine deposits with most finds in terrestrial deposits from the Late Devonian and the Late Triassic.

Introduction

The Devonian to Triassic strata of East Greenland are preserved in well-exposed terrestrial basins which have been extensively examined for terrestrial fossil remains since the 19th century. The first tetrapod

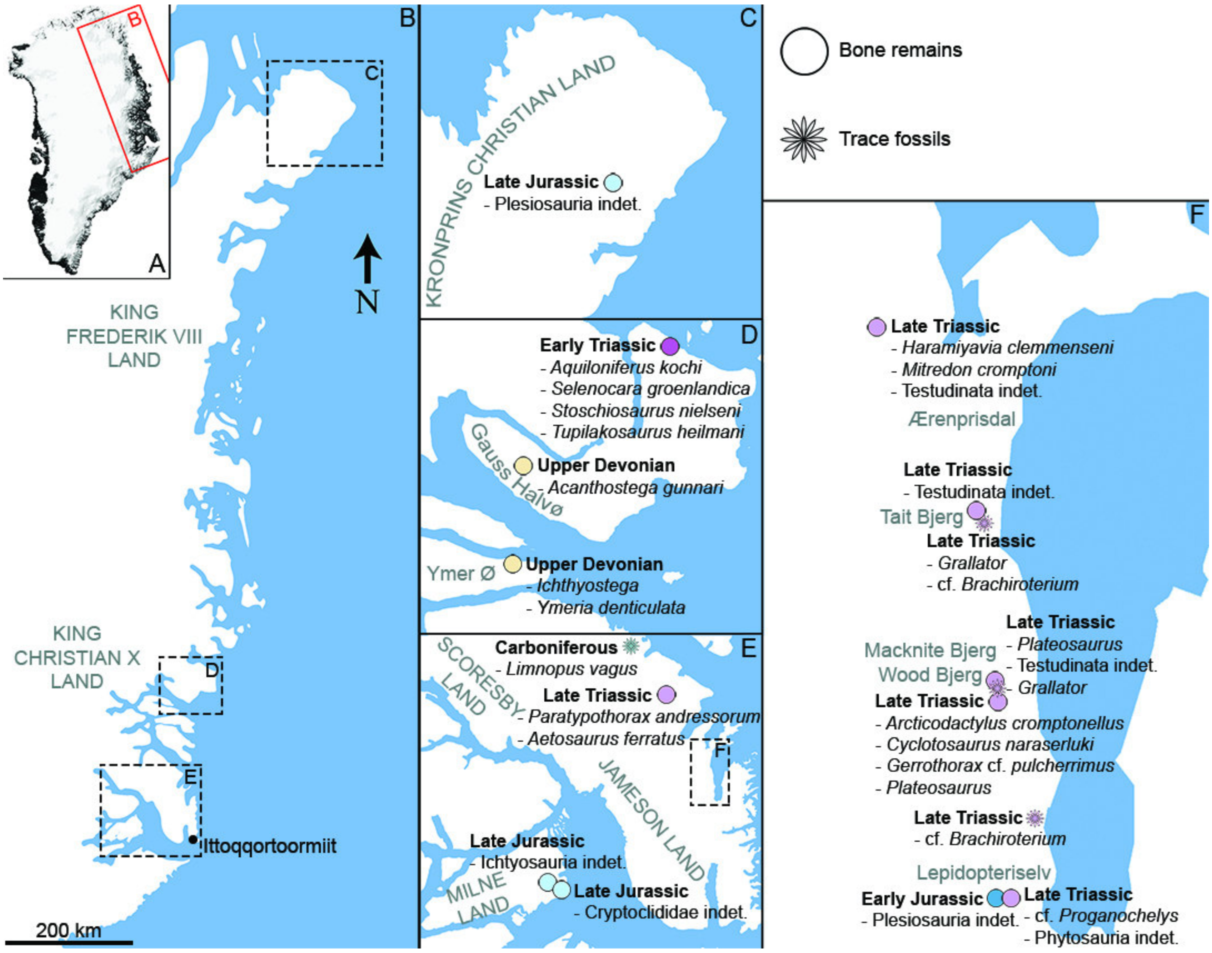

Figure 1.1 - A–F: Maps showing the position of the main fossil tetrapod sites of Greenland.

discoveries in Greenland are recorded from the Devonian of Ymer Ø (East Greenland, Fig. 1.1), found during an expedition in 1899 led by the Swedish naturalist and Arctic explorer Alfred Gabriel Nathorst (Nathorst 1900, 1901; Woodward 1900). From the late 1920s until at least 1955, the Devonian of East Greenland was the target of several palaeontological expeditions (Heintz 1930, 1932; Koch 1930; Orvin & Heintz 1930; Stensiö 1931; Säve-Söderbergh 1932; Ries 2002; Blom et al. 2007). The Devonian outcrops of East Greenland also shed light on the first stem tetrapod ever found and described from Greenland: *Ichthyostega* Säve-Söderbergh 1932, a milestone fossil recovered in 1929 (Stensiö 1931). A few years later, the Devonian of East Greenland provided vertebrate palaeontologists with a second milestone stem tetrapod for understanding the transition from fishes to tetrapods: *Acanthostega gunnari* Jarvik 1952. New expeditions also took place during the early 1970s, one of which, led by P.F. Friend from the University of Cambridge, discovered new tetrapod material (Friend et al. 1976). These were followed by expeditions in 1987 and 1998 which recovered much more material (Clack 1988a, b; Bendix-Almgreen et al. 1990, Marshall et al. 1999, Clack & Neininger 2000; Clack et al. 2012) (Fig. 1.1D). During the earliest expeditions, tetrapod fossils were discovered in the Early Triassic of the

Wordie Creek Group (e.g. Säve-Söderbergh 1935; Nielsen 1954, 1967). Extensive stratigraphical studies of the Mesozoic strata in the Jameson Land area were carried out in the late 1960s and early 1970s and led to the discovery of a few vertebrate fossils, including temnospondyl remains in Middle and Late Triassic strata (e.g. Clemmensen 1980b). Moreover, at the beginning of the 1970s the Mesozoic sediments of the eastern Milne Land were mapped and a couple of Late Jurassic neodiapsid marine reptiles were reported (Håkansson et al. 1971).

From the late 1980s, East Greenland saw new explorative initiatives aimed at recovering fossil tetrapod material by Harvard University (Massachusetts, USA) in collaboration with the University of Copenhagen (Denmark). These expeditions, led by the late Farish Jenkins, took place from 1988 to 2001 and explored the Late Triassic of the Jameson Land Basin (Fig. 1.1F); they acquired a plethora of unique tetrapods such as temnospondyls, testudinatans, pterosaurs, dinosaurs and the early mammal Haramiyavia clemmenseni Jenkins et al. 1997 (see also Jenkins et al. 1994, 2001, 2008; Gatesy et al. 1999; Shapiro & Jenkins 2001; Sulej et al. 2014; Clemmensen et al. 2016).

The latest expeditions that collected fossil tetrapods from Greenland were undertaken in 2012 and 2016 by the GeoCenter Møns Klint Dinosaur Expeditions, and in 2014 by a Polish-Danish team, recovering testudinatans, phytosaurs, dinosaurs, stem mammals and various vertebrate tracks from the Late Triassic of different fossiliferous sites in the Jameson Land Basin (Milàn et al. 2004, 2006, 2012; Mateus et al. 2014; Sulej et al. 2014; Clemmensen et al. 2016; Hansen et al. 2016; Kear et al. 2016a; Klein et al. 2016; Marzola et al. 2016, 2017a; Lallensack et al. 2017; Niedzwiedzki & Sulej 2017). Expeditions to the Celsius Bjerg Group, Wordie Creek Group and Fleming Fjord Formation of East Greenland were also launched by Uppsala University (Sweden) in 2015 and 2016, with vertebrate fossils recovered from various sites (Benjamin Kear, personal communication 2017).

We use the lithostratigraphical schemes by Clack & Neininger (2000) for the Celsius Bjerg Group (Fig. 1.1D), Surlyk et al. (2017) for the Wordie Creek Group (Fig. 1.1D), and Clemmensen (1980b) for the Fleming Fjord Formation (Fig. 1.1E–F).

This article aims to give an updated systematic list and photographic review of the known Palaeozoic and Mesozoic fossil tetrapod occurrences from Greenland (Figs. 1.1–1.2). We also give the first formal report on plesiosaur remains from the Late Jurassic Kuglelejet Formation (Dypvik et al. 2002) at Kilen, Kronprins Christian Land (Fig. 1.1C).

Environmental context

Tetrapod fossils were recovered from at least three main sedimentary basins in Greenland, all of which are connected to extensive tectonic events and successive sedimentary infills. The Late Devonian Celsius Bjerg Group is the fourth and youngest stratigraphic division of the continental Old Red Sandstone Basin in East Greenland. This basin was formed during the Middle to Late Devonian, mainly by extensional collapse of an over-thickened Caledonian crustal welt (Larsen et al. 2008). Fossil-bearing horizons include the Aina Dal Formation, characterised by meandering river deposits, and the Britta Dal Formation, distinguished by ephemeral stream and flood basin deposits (Larsen et al. 2008).

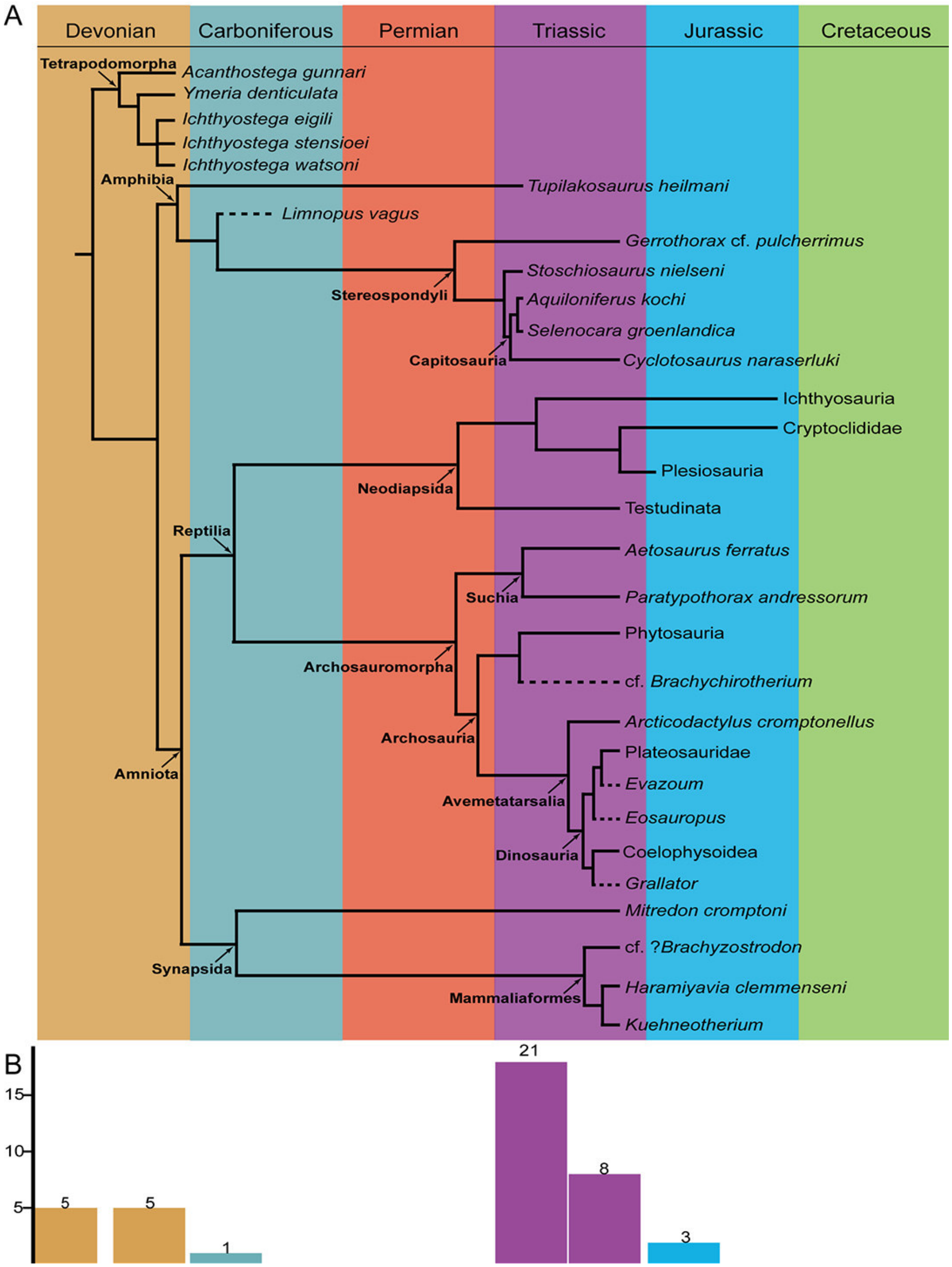

Figure 1.2 - Main fossil tetrapod taxa of Greenland. A: Time calibrated phylogenetic cladogram with major nodes enlightened with arrows and bold headings (for major clades relationships see Ruta et al. 2007; Schoch 2008; Brusatte et al. 2011; Clack et al. 2012; Benton 2014). Dashed lines stand for ichnotaxa. B: Alpha diversity (number of taxa per period). Left bars indicate the number of taxa in the fossil record; when present, right bars indicate the number of endemic species of Greenland.

During the Middle to Late Devonian, East Greenland was located around 5–10°N, forming part of the equatorial Laurasia continent, and likely included a trade wind belt with monsoonal climate during the summer (Olsen 1990; Larsen et al. 2008). Greenland drifted north during the entire Palaeozoic era, and during the Early–Middle Triassic the East Greenland basins were situated at a latitude of ~25°N and were characterised by an arid paleoclimate (Kent & Clemmensen 1996). Northward drift continued, and in the Late Triassic the Jameson Land Basin reached 40°N and was situated at the boundary between a subtropical arid and a winter-wet, warm temperate climate belt (Kent & Clemmensen 1996; Clemmensen et al. 1998; Kent & Tauxe 2005). Continued northward drift during the Jurassic changed the climate in the Jameson Land and nearby basins to warm temperate and humid.

The Triassic continental Jameson Land Basin is situated in the southern part of the East Greenland rift system and has been interpreted as an open embayment with a N–S orientation. The basin developed by extension and subsidence episodes during both the Late Permian to Early Triassic and the Late Triassic (Clemmensen 1980a, b; Price & Whitham 1997; Wignall & Twitchett 2002; Larsen et al. 2008). Characterised during the first stages of the Early Triassic by marine conditions, the Jameson Land Basin records regressions and continental emergence later in the Early Triassic (Clemmensen 1980a, b; Wignall & Twitchett 2002; Nøttvedt et al. 2008). Tetrapod fossils are found in the Jameson Land Basin in the mainly marine Early Triassic Wordie Creek Group, in the Late Triassic Fleming Fjord Formation characterised by freshwater lake deposits, and in the Late Triassic to Jurassic Kap Stewart Formation interpreted as a lacustrine depositional system (Clemmensen 1980a; Dam & Surlyk 1992; Clemmensen et al. 1998, 2016; Wignall & Twitchett 2002; Larsen et al. 2008).

Milne Land (Fig. 1.1E) is characterised by Jurassic marine sediments that directly overlie the Caledonian crystalline basement; the sediments were deposited during the Bathonian, due to the opening of the proto-Atlantic seaway between Greenland and Norway (Callomon & Birkelund 1980). Fossil tetrapods have been found in the Kap Leslie Formation, which is composed of marine sandstones and shales (Callomon & Birkelund 1980).

Devonian

Skeletal fossils

***Acanthostega gunnari* Jarvik 1952** (Stegocephali: Acanthostegidae)

Holotype. NHMD 74758 (previously MGUH A33 in Coates 1996 and previously MGUH VP 6264), a partial skull (Fig. 1.3).

Localities. Wiman Bjerg & Stensiö Bjerg, Gauss Halvø (Fig. 1.1D).

Horizon. Britta Dal Formation, Celsius Bjerg Group, fluvial deposits; low-latitude monsoonal climate.

Age. Late Devonian (Famennian).

Selected bibliography. Clack (1988a, 1989, 1992, 1994, 1998, 2002a, b); Coates (1996); Ahlberg & Clack (1998); Marshall et al. (1999); Clack et al. (2003); Larsen et al. (2008); Neenan et al. (2014).

Comments. We report here only the holotype. Coates (1996) reported at least 14 different specimens ascribed to *Acanthostega*.

***Ichthyostega* Säve-Söderbergh 1932** (Tetrapodomorpha: Ichthyostegidae)

Holotypes. *I. eigili* Säve-Söderbergh 1932 - MGUH VP 6004, an almost complete skull (Fig. 1.4); *I. stensioi* Säve- Söderbergh 1932 - MGUH VP 6001, a partial skull with skull roof and anterior palate (Fig. 1.5); *I. watsoni* Säve-Söderbergh 1932 - MGUH VP 6003, an almost complete skull (Fig. 1.6).

Locality. East Plateau at the north side of Celsius Bjerg, Ymer Ø (Fig. 1D).

Horizon. Aina Dal Formation and Britta Dal Formation, Celsius Bjerg Group, fluvial deposits; low-latitude monsoonal climate. Age. Late Devonian (Famennian).

Selected bibliography. Jarvik (1952, 1996); Marshall et al. (1999); Ahlberg et al. (2005); Blom (2005); Ahlberg & Clack (2006); Larsen et al. (2008); Pierce et al. (2012, 2013).

Comments. We report here only the holotypes' depository numbers. As noted by Blom (2005) over 300 specimens are referred to *Ichthyostega*. The species name for *I. stensioi* is given following the spelling of Snitting & Blom (2009).

Figure 1.3 - The stem tetrapod *Acanthostega gunnari* Jarvik 1952, holotype NHMD 74758 (previously MGUH VP 6033, MGUH A33 in Coates 1996 and previously MGUH VP 6264): partial skull in dorsolateral view, from the Late Devonian of the Britta Dal Formation. Scale bar: 5 cm.

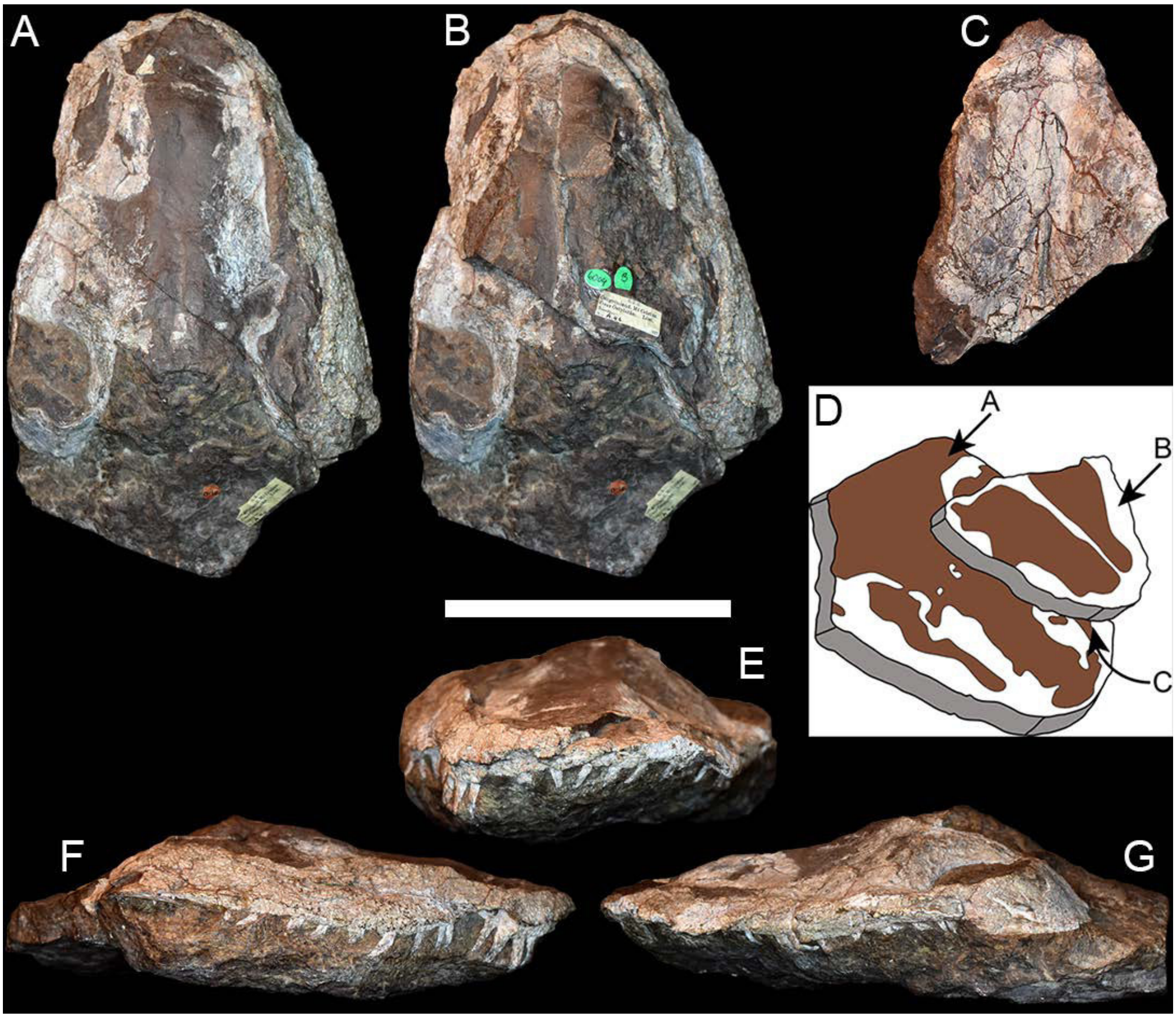

Figure 1.4 - The stem tetrapod *Ichthyostega eigili* Säve- Söderbergh 1932, holotype MGUH VP 6004 from Late Devonian of the Aina Dal and Britta Dal Formations. A–B: Dorsal views C: Ventral view. D: Schematic drawing of MGUH VP 6004 with correspondent views of A, B, and C, out of scale and with exaggerated thickness. E: Frontal view. F: Right lateral view. G: Left lateral view. Scale bar A–C, E–G: 10 cm.

Ymeria denticulata Clack et al. 2012 (Tetrapodomorpha: Tetrapoda)

Holotype. NHMD 74759 (previously MGUH VP 6088), a partial skeleton with cranial elements (lower jaws, maxillae, premaxillae, partial palate) and postcranial shoulder girdle (Fig. 1.7).

Locality. South side of Celsius Bjerg, Ymer Ø (Fig. 1.1D).

Horizon. Celsius Bjerg Group, scree (fluvial deposits); low-latitude monsoonal climate.

Age. Late Devonian (Famennian).

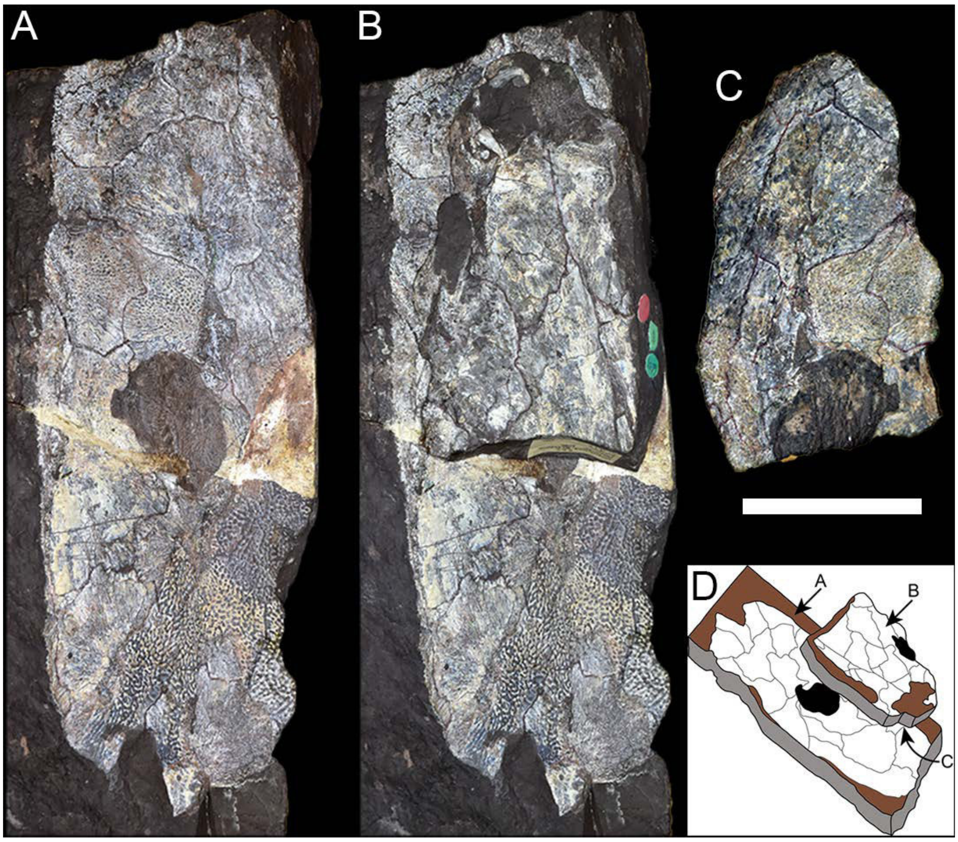

Figure 1.5 - The stem tetrapod *Ichthyostega stensioi* Säve- Söderbergh 1932, holotype MGUH VP 6001: partial skull from Late Devonian of the Aina Dal and Britta Dal Formations. A–B: Dorsal views. C: Ventral view. D: Schematic drawing of MGUH VP 6001 with correspondent views of A, B, and C, out of scale and with exaggerated thickness. Scale bar A–C: 5 cm.

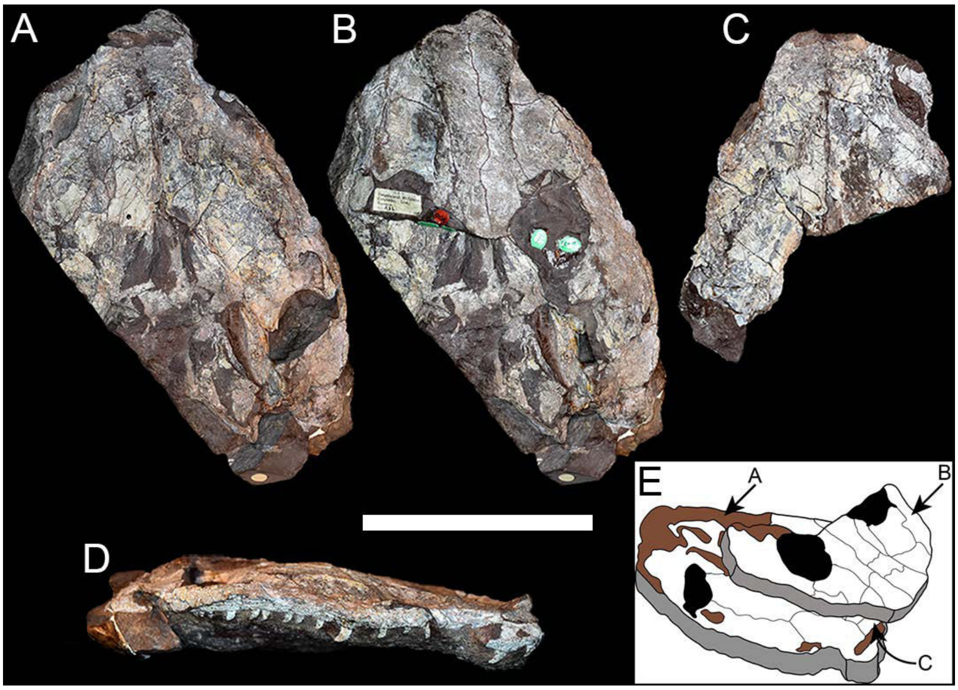

Figure 1.6 - The stem tetrapod *Ichthyostega watsoni* Säve- Söderbergh 1932, holotype MGUH VP 6003: partial skull from Late Devonian of the Aina Dal and Britta Dal Formations. A–B: Dorsal views. C: Ventral view. D: Right lateral view. E: Schematic drawing of MGUH VP 6001 with correspondent views of A, B, and C, out of scale and with exaggerated thickness. Scale bar A–D: 10 cm.

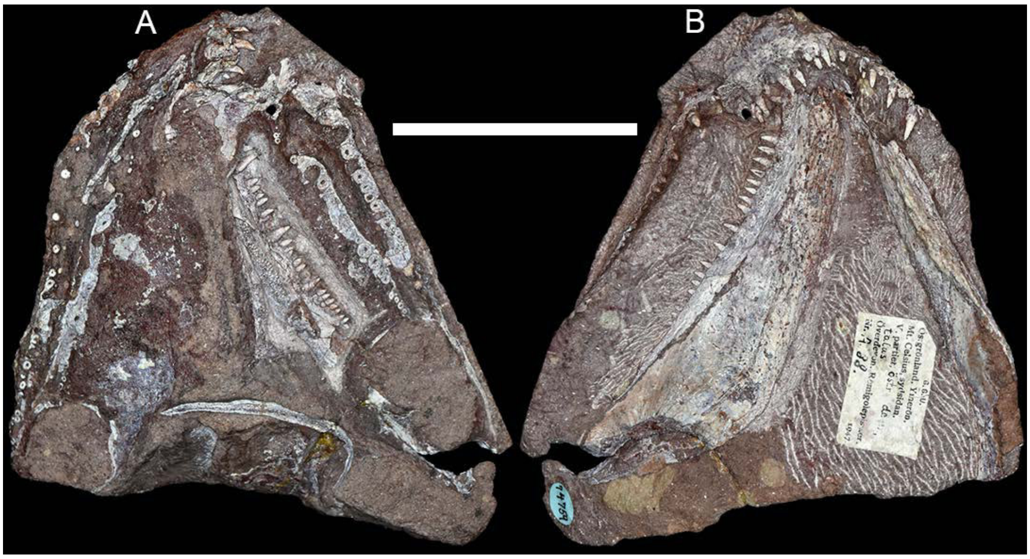

Figure 1.7 - The stem tetrapod *Ymeria denticulata* Clack et al. 2012, holotype NHMD 74759 (previously MGUH VP 6088), a partial skull with lower jaws from Late Devonian of the Britta Dal Formation. A: Dorsal view. B: Ventral view. Scale bar: 5 cm.

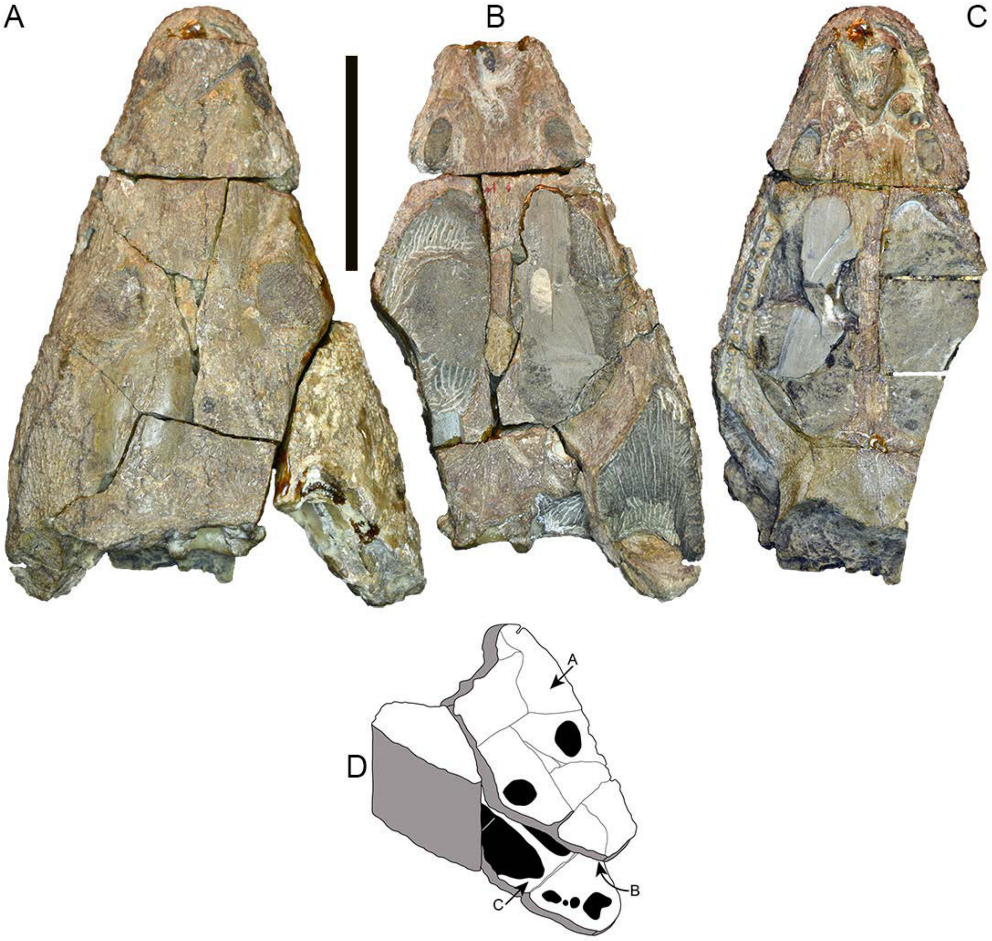

Figure 1.8 - The capitosauroid *Aquiloniferus kochi* Bjerring 1999, holotype MGUH VP 3357 (previously MGUH VP At.1): a skull from the Early Triassic of the Wordie Creek Group. A, C: Dorsal views. B: Ventral view. D: Schematic drawing of MGUH VP 3357 with correspondent views of A, B, and C (out of scale and with exaggerated thickness). Scale bar A–C: 5 cm.

Carboniferous

Skeletal fossils

Limnopus vagus Marsh 1894

Referred material. MGUH 31556, a slab preserving at least 12 tracks (isolated and three as pes-manus couples) on average 50 to 55 mm long and 55 to 70 wide.

Locality. Langelinie mountain, Mesters Vig, northern Scoresby Land, 72°09 N, 24°07 W (Fig. 1.1E).

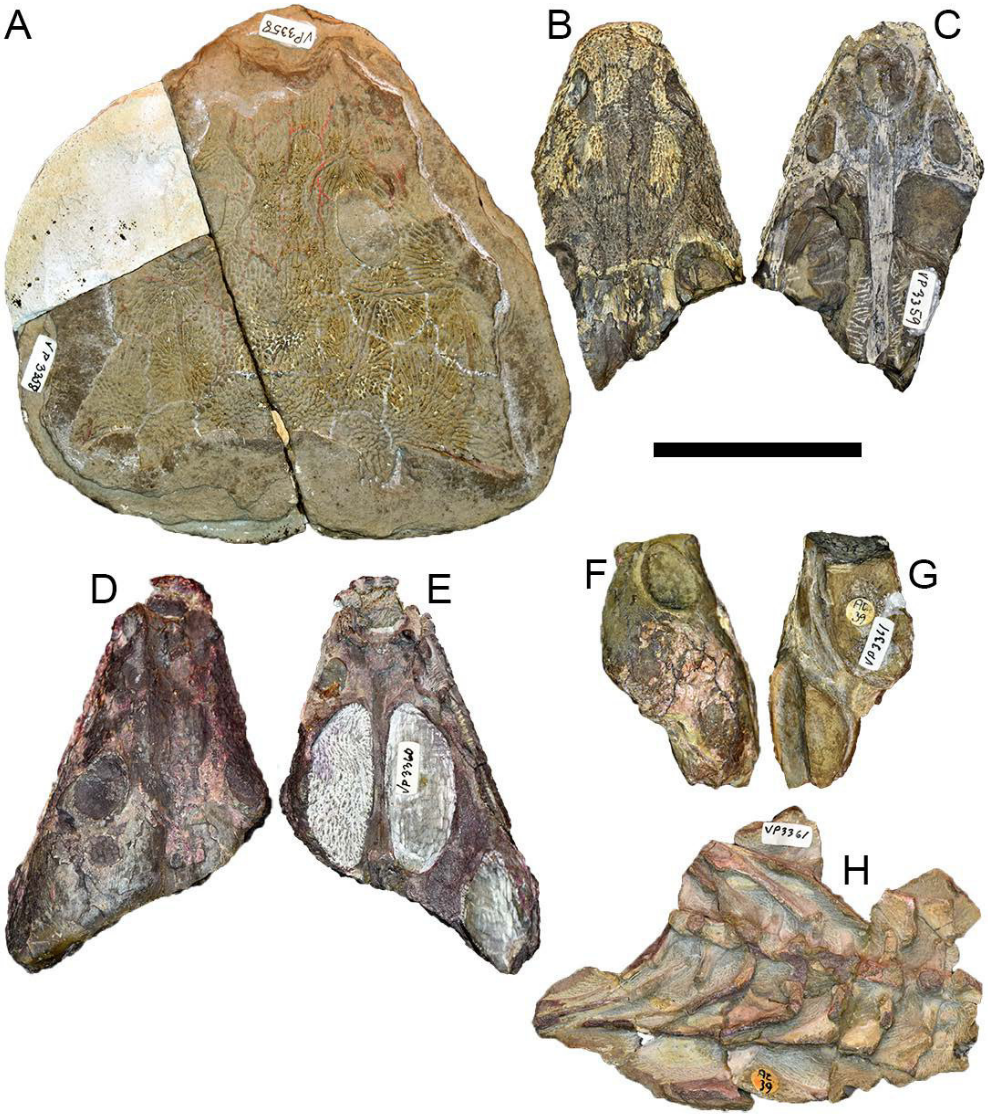

Figure 1.9 - The capitosauroid *Aquiloniferus kochi* Bjerring 1999: specimens from the Early Triassic of the Wordie Creek Group. A: Dorsal view of MGUH VP 3358 (previously MGUH VP At. 3), natural internal cast of a partial skull. B–C: Dorsal and ventral views of MGUH 3359 (previously MGUH VP At. 28), a partial skull. D–E: Dorsal and ventral views of MGUH 3360 (previously MGUH VP At. 29), a partial skull. F–H: MGUH 3361 (previously MGUH VP At. 39), as a partial skull, in dorsal (F) and ventral (G) views, and seven cervical vertebrae (H). Scale bar: 5 cm.

Horizon. Non-marine dark brown, fine- to mediumgrained sandstone from floodplain deposits of either Blyklippen or Profilbjerget Member of the Mesters Vig Formation, Traill Ø Group.

Age. Late Carboniferous (late Bashkirian to early Moscovian).

Selected bibliography. Bendix-Almgreen (1976); Milàn et al. (2016a).

Comments. The tracks were originally found by E. Witzig during field work in 1950. These tracks, together with additional material, were first depicted by Bendix-Almgreen (1976, p. 553, fig. 425D) and described as casts of tetrapod trails. However, Bendix-Almgren (1976) erroneously reported them as Lower Permian. Gilberg (1992) re-mentioned them briefly in a firsthand account from the fieldwork in 1950. Milàn et al. (2016a) indicated eryopoid temnospondyls as the potential track makers.

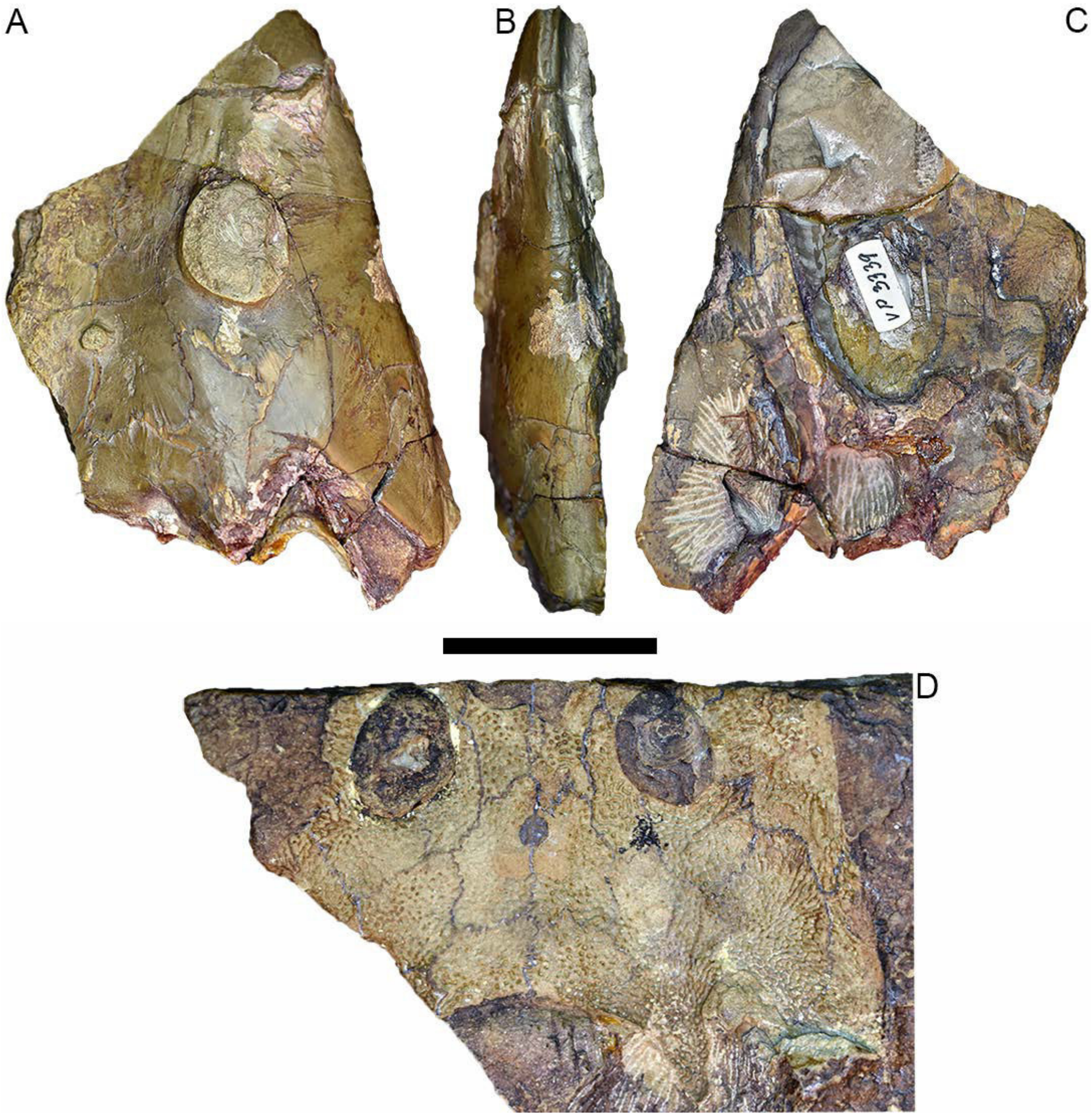

Figure 1.10 - The capitosaurid *Selenocara groenlandica* Bjerring 1997, holotype MGUH VP 3339 (previously MGUH VP At. 2): a partial skull from the Early Triassic of the Wordie Creek Group, in A: Dorsal views, B: Lateral right view, and C: Ventral views; and natural cast of partial skull MGUH VP 3340 (previously MGUH VP At. 17) (D), from the Early Triassic of the Wordie Creek Group in D: dorsal view. Scale bar: 3 cm.

Triassic

Skeletal fossils

***Aquiloniferus kochi* Bjerring 1999** (Temnospondyli: Capitosauroidea)

Holotype. MGUH VP 3357 (previously MGUH VP At.1), a skull (Fig. 1.8).

Referred material. MGUH VP 3358 (previously MGUH VP At. 3), a natural internal cast of a partial skull; MGUH 3359 (previously MGUH VP At. 28), a partially preserved anterior half of a skull; MGUH 3360 (previously MGUH VP At. 29), a partially preserved skull; MGUH 3361 (previously MGUH VP At. 39), a partially preserved skull associated to seven cervical vertebrae (Fig. 1.9).

Locality. South-east of Kap Stosch, Stensiö Plateau and Spath Plateau, Hold With Hope (Fig. 1.1D). Horizon. Myalina kochi horizon, Wordie Creek Group, shallow marine deposits; warm tropical climate.

Age. Early Triassic (Induan).

Selected bibliography. Cosgriff (1984); Lucas (1998); Bjerring (1999).

Comments. These specimens were originally attributed to *Luzocephalus johanssoni* Säve-Söderbergh 1935.

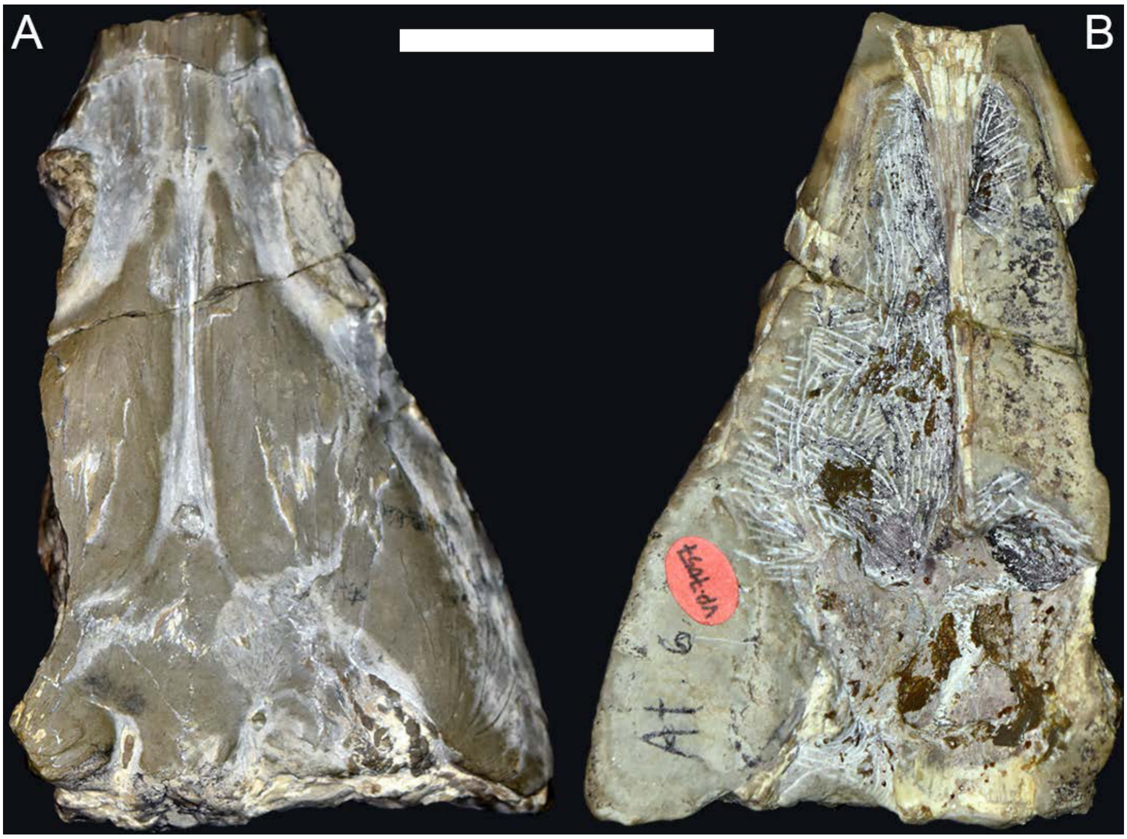

Figure 1.11 - The trematosaurid *Stoschiosaurus nielseni* Säve-Söderbergh 1935, holotpye MGUH VP 7057 (previously MGUH VP At.6): a partial skull. A: Dorsal view. B: Ventral view. Scale bar: 3 cm.

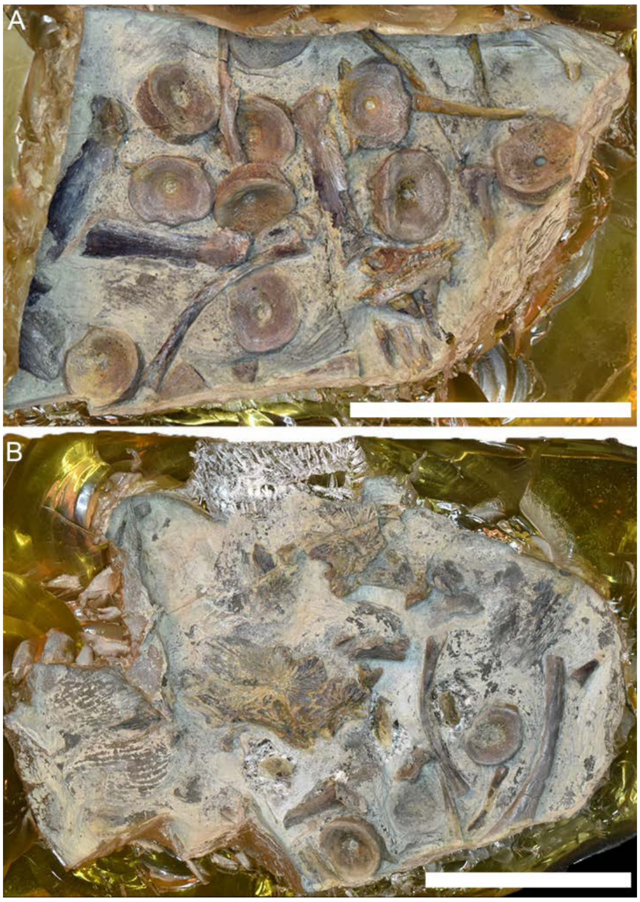

Figure 1.12 - The tupilakosaurid *Tupilakosaurus heilmani* Nielsen 1954, holotype MGUH VP 3328 (specimen A): two separate blocks containing postcranial material (including vertebrae, ribs, tooth) from the Early Triassic of the Wordie Creek Group. A: Block A. B: Block B. Scale bars: 5 cm.

***Selenocara groenlandica* Bjerring 1997** (Temnospondyli: Capitosauroidea)

Holotype. MGUH VP 3339 (previously MGUH VP At. 2), posterior part of a skull (Fig. 1.10).

Referred material. MGUH VP 3340 (previously MGUH VP At. 17), a natural cast of a partial skull.

Locality. South-east of Kap Stosch, ridge VIII–IX of the north-east slope of Stensiö Plateau, Hold With Hope (Fig. 1D).

Horizon. Myalina kochi horizon, Wordie Creek Group, shallow marine deposits; warm tropical climate.

Age. Early Triassic (Induan). Selected bibliography. Bjerring (1997); Lucas (1998).

Comments. These specimens were originally identified as *Wetlugasaurus groenlandicus* by Säve-Söderbergh (1935).

Stoschiosaurus nielseni Säve-Söderbergh 1935 (Temnospondyli: Trematosauridae)

Holotype. MGUH VP 7057 (previously MGUH VP At.6), a partial skull (Fig. 1.11).

Locality. South-east of Kap Stosch, ridge VIII–IX of the north-east slope of Stensiö Plateau, Hold With Hope (Fig. 1.1D).

Horizon. Myalina kochi horizon, Wordie Creek Group, coastal claystone/sandstone, shallow marine deposits; warm tropical climate.

Age. Early Triassic (Induan).

***Tupilakosaurus heilmani* Nielsen 1954** (Temnospondyli: Tupilakosauridae)

Holotype. MGUH VP 3328 (specimen A), a partial skeleton (Fig. 1.12).

Locality. South-east of Kap Stosch, north-east slope of Stensiö Plateau, Hold With Hope (Fig. 1.1D).

Horizon. Myalina kochi horizon, Wordie Creek Group, shallow marine deposits; warm tropical climate.

Age. Early Triassic (Induan). Selected bibliography. Nielsen (1954, 1967).

***Cyclotosaurus naraserluki* Marzola et al. 2017b** (Temnospondyli: Cyclotosauridae)

Holotype. MGUH.VP 9522, a nearly complete skull (Fig. 1.13A).

Referred material. Two vertebral intercentra, MGUH. VP 9523 and MGUH.VP 9524.

Locality. Macknight Bjerg, Jameson Land, 71°22.30′ N, 22°33.14′ W (Fig. 1.1F).

Horizon. Ørsted Dal Member (Carlsberg Fjord beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Marzola et al. (2017b).

***Gerrothorax cf. pulcherrimus* Fraas 1913** (Temnospondyli: Plagiosauridae)

Referred material. At least sixty-four specimens of *G. pulcherrimus* have been recovered from the Fleming Fjord Formation. The main specimens used for the descriptions in Jenkins et al. (2008) are MGUH 28916, MGUH 28917, MGUH 28918, MGUH 28919, MGUH 28921, MGUH 28923 and MGUH 28925 for skull anatomy and interclavicles; MGUH 28922 and MGUH 28924 for vertebral structure and dermal armour.

Locality. Macknight Bjerg, Jameson Land, 71°22.30′ N, 22°33.14′ W (Fig. 1.1F).

Horizon. Ørsted Dal Member (Carlsberg Fjord beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994, 2008); Schoch & Witzmann (2012); Sulej et al. (2014).

cf. *Proganochelys* Baur 1887 (Testudinata: Proganochelyidae)

Referred material. NHMD 190349 (previously MCZ Field no. 22/88G), partially preserved carapace and plastron, caudal vertebrae, and incomplete limb bones (right humerus, right ulna, right radius, both femora, and left tibia) (Fig. 1.13C).

Locality. Lepidopteriselv, Jameson Land, 71°15.760′ N, 22°32.682′ W, 285 m a.s.l. (Fig. 1.1F)

Horizon. Upper part of the Ørsted Dal Member (Carlsberg Fjord Beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Marzola et al. (2016).

Comments. This specimen was originally described by Jenkins et al. (1994) as cf. *Proganochelys*, based on two presumed autapomorphies for the genus *Proganochelys*: (1) the presence of a pair of gular and intergular projections and (2) the presence of the dorsal epiplastral process. Paired gular projections are now also known in the Late Triassic *Odontochelys semitestacea* Li et al. (2008) from China, while dorsal epiplastral processes are known both in *O. semitestacea* and the Early Jurassic *Kayentachelys aprix* Gaffney et al. (1987) from Arizona, USA. An expedition to the Jameson Land Basin in the summer of 2016 (Marzola et al. 2017a) revisited the source locality and collected additional components of the specimen including two fragmentary vertebrae.

Testudinata indet.

Referred specimen. NHMD 163391–163417, a fragmentary specimen including carapace, plastron, scapular and pelvic girdles, and limb bones; NHMD 74737, a fragmentary specimen including carapace, plastron, and pelvic girdle.

Locality. NHMD 163391–163417 was found during the US-Danish expedition in 1995 at Ærenprisdal, Jameson Land, 71°32.611′ N, 22°55.307′ W; NHMD 74737 was found during the Danish expedition in 2012 by one of us (OM) in solifluction at Wood Bjerg–Macknight Bjerg, Jameson Land, 71°22.965′ N, 22°33.216′ W (Fig. 1.1F).

Horizon. NHMD 163391–163417 and NHMD 74737 both come from the Ørsted Dal Member (Carlsberg Fjord beds) of the Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Mateus et al. (2014); Clemmensen et al. (2016); Marzola et al. (2016).

Comments. Both specimens are unpublished and are currently under study. Another specimen has been found by the Cambridge expedition in 2015, from the Malmros Klint or Ørsted Dal Member of the Fleming Fjord Formation (Steven Andrews, personal communication 2016).

***Aetosaurus ferratus* Fraas 1877** (Archosauria: Stagonolepididae)

Referred material. NHMD 190375–190379 (previously MCZ Field no. 22/92G), a skull associated with dermal armor, limb bones, vertebrae, and a partial sacrum (Fig. 1.13B).

Locality. Sydkronen, northern Jameson Land, 71°49.65′ N, 23°30.83′ W (Fig. 1.1E).

Horizon. Ørsted Dal Member (Bjergkronerne beds), Fleming Fjord Formation, fluvial deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Schoch (2007); Parker (2016).

Comments. Despite being incomplete, this specimen has been attributed to *A. ferratus* by most recent studies (Schoch 2007; Parker 2016).

***Paratypothorax andressorum* Long & Ballew 1985** (Archosauria: Stagonolepididae)

Referred material. MCZ Field no. 23/92G, one paramedian (mostly preserved as a natural mold) and two lateral dermal scutes.

Locality. Sydkronen, northern Jameson Land. Horizon. Uncertain, potentially Ørsted Dal Member, Fleming Fjord Formation, fluvial deposits; subtropical arid to winter-wet, warm temperate climate.

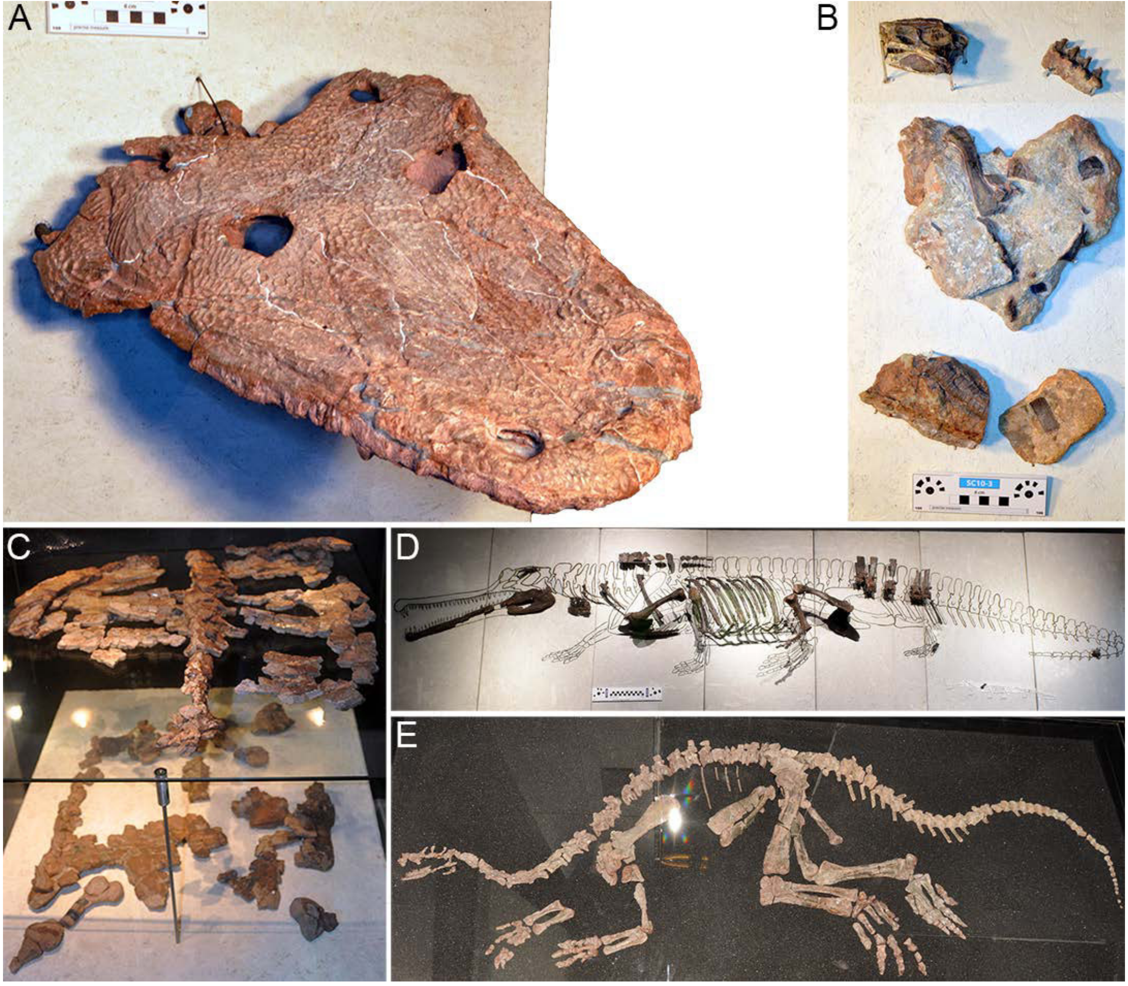

Figure 1.13 - Fossil tetrapods from the Late Triassic of Jameson Land Basin in exhibition at the GeoCenter of Møns Klint, Denmark, as of 2016. A: Oblique photograph of the holotype of the capitosaurid *Cyclotosaurus naraserluki* Marzola et al. 2017b MGUH.VP 9522. B: The stagonolepidid *Aetosaurus ferratus* Fraas 1877 NHMD 190375–190379 (previously MCZ Field no. 22/92G). C: Oblique photograph of the Testudinata NHMD 190349 (previously MCZ Field no. 22/88G) (top layer: carapace; bottom layer: plastron and limb bones). D: Adult and juvenile (bottom right corner) phytosaurs, respectively NHMD 74733 and NHMD 74736. E: Sauropodomorph plateosauridae NHMD 164734 (previously 4/88/G and GM.V 2013-683). C and E not scaled. Scale bars, A–B: 6 cm; D: 15 cm.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Lucas et al. (2006).

Phytosauria indet. (Archosauriformes: Crurotarsi)

Referred specimen. Four incomplete phytosaurs (two adults, one subadult and one juvenile) collected during the 2012 GeoCenter Møns Klint expedition (NHMD 74733–74736, Fig. 1.13D).

Locality. 'Mateus' site, Lepidopteriselv, Jameson Land, 71°15.584′ N, 22°31.785′ W (Fig. 1.1F).

Horizon. Middle Malmros Klint Member, Fleming Fjord Formation, lacustrine and overbank fluvial deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Mateus et al. (2014); Clemmensen et al. (2016).

***Arcticodactylus cromptonellus* (Jenkins et al. 2001)** (Pterosauria: Eudimorphodontidae)

Holotype. NHMD 74799, a disarticulated skeleton preserving numerous cranial and postcranial elements (Fig. 1.14).

Locality. Macknight Bjerg, Jameson Land, 71°22.277′ N, 22°33.341′ W (Fig. 1.1F).

Horizon. Ørsted Dal Member (Carlsberg Fjord beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Dalla Vecchia (2003, 2014); Kellner (2015).

Comments. Originally attributed by Jenkins et al. (1994) to the genus *Eudimorphodon* Zambelli 1973, this specimen was later described as a new genus, *Arcticodactylus*, by Kellner (2015).

Plateosauridae *indet*. (Dinosauria: Sauropodomorpha)

Referred material. At least four individuals: NHMD 164734 (previously 4.88.G and GM.V 2013-683), an unreported and unpublished complete individual with cranial and postcranial material (Fig. 1.13E); NHMD 164741 (previously MCZ Field no. 61/91G), a skull reported in Jenkins et al. (1994, fig. 11, p. 14); NHMD 164758 (previously 1/G95 or 1/95/G), an unreported and unpublished individual with cranial and postcranial material, probably a sub-adult; NHMD 164775, unpublished and partially unprepared material excavated during the 2012 Danish expedition.

Locality. NHMD 164734 is from Lepidopteriselv, Jameson Land; NHMD 164741 and NHMD 164758 are from the north side of Macknight Bjerg, Jameson Land, with the former located at 71°23.010′ N, 22°34.114′ W and the latter stratigraphically slightly above it, at 71°22.993′ N, 22°33.972′ W; NHMD 164775 is from the 'Iron Cake' Site, Wood Bjerg–Macknight Bjerg, Jameson Land, 71°22.262′ N, 22°33.381′ W (Fig. 1.1F).

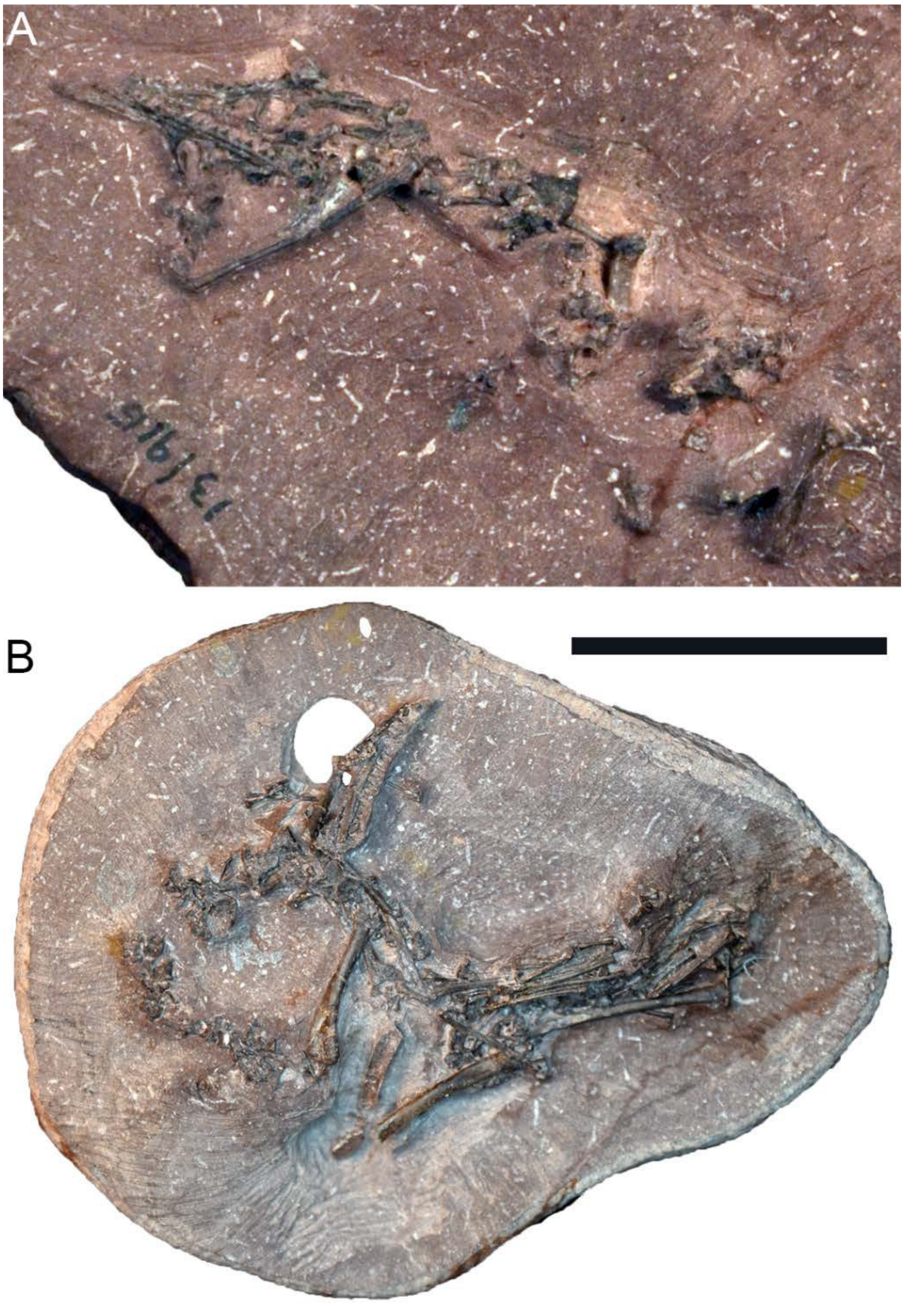

Figure 1.14 - The eudimorphodontid *Arcticodactylus cromptonellus* (Jenkins et al. 2001), holotype NHMD 74799 from the Late Triassic of the Fleming Fjord Formation. A: block exposed in the GeoCenter (as for 2016). B: counter block at NHMD. Scale bar: 3 cm.

Horizon. NHMD 164734 is from the Ørsted Dal Member (Carlsberg Fjord beds), Fleming Fjord Formation, NHMD 164741 and 164758 from the uppermost Malmros Klint Member, Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Clemmensen et al. (2016).

Comments. As of August 2017, NHMD 164734 is exhibited at GeoCenter Møns Klint, Denmark (Fig. 13E); NHMD 164741 and the skull of NHMD 164758 are under restoration and final preparation at Museu da Lourinhã (Portugal), while the postcranial material of NHMD 164758 is in storage at GeoCenter Møns Klint; a partially prepared rib cage of NHMD 164775 is also exhibited at GeoCenter Møns Klint, while the rest of the material from the 2012 expedition is stored and under preparation at Dino-Park Münchehagen (Germany). Jenkins et al. (1994) associated NHMD 164741 to *Plateosaurus engelhardti*. We suggest that this association is considered with caution because preliminary phylogenetic studies by our team indicate that this specimen belongs to the clade Plateosauria, though presenting distinct and unique morphological characters that distinguish it from *Plateosaurus*.

***Mitredon cromptoni* Shapiro & Jenkins 2001** (Therapsida: Cynodontia)

Holotype. MGUH VP 3392, an incomplete left mandible with teeth (Fig. 1.15).

Locality. North of Ærenprisdal at its junction with Pingel Dal, Jameson Land, 71°32.929′ N, 22°55.450′ W (Fig. 1.1F).

Horizon. Uppermost dolostone in Ørsted Dal Member (Tait Bjerg Beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Shapiro & Jenkins (2001).

cf. ?*Brachyzostrodon* Sigogneau-Russell 1983 (Mammalia: Morganucodontidae)

Referred specimen. MCZ Field no. 64/91 G 4, a mammaliamorph tooth.

Locality. Western slope of Tait Bjerg, Jameson Land, bounded by Passagen to the south, Buch Bjerg to the north, and Carlsberg Fjord to the east.

Figure 1.15 - The cynodont *Mitredon cromptoni* Shapiro & Jenkins 2001, holotype MGUH VP 3392: a left dentary from the Late Triassic of the Fleming Fjord Formation. A: lingual view. B: labial view. Scale bar: 1 cm.

Horizon. Dolomitic limestone of the Tait Bjerg Beds, Ørsted Dal Member of the Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994).

***Haramiyavia clemmenseni* Jenkins et al. 1997** (Mammalia: Haramiyidae)

Holotype. MCZ 7/95, partially associated cranial elements and postcranial bones, including dentaries, premaxilla, vertebrae, and limb bones (Fig. 1.16A–B).

Referred specimen. MCZ 10/95, a left mandible with teeth (Fig. 1.16C).

Locality. North side of Ærenprisdal, at the junction with Pingel Dal, Jameson Land, 71°32.958′ N, 22°55.188′ W, 670 m a.s.l. (Fig 1.1F).

Horizon. Ørsted Dal Member (Tait Bjerg Beds), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Luo et al. (2015).

***Kuehneotherium* Kermack et al. 1968** (Mammalia: Kuehneotheriidae)

Referred specimen. MCZ Field no. 62/91 G 1–2 and 64/91 G 3–8 and 10: ten mammaliamorph teeth.

Locality. Western slope of Tait Bjerg, Jameson Land, bounded by Passagen to the south, Buch Bjerg to the north, and Carlsberg Fjord to the east.

Horizon. Ørsted Dal Member (Tait Bjerg Beds, dolomitic limestone), Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994).

Comments. Two teeth (MCZ 62/91 G 1–2) were found in the lowermost Ørsted Dal Member (Carlsberg Fjord beds), while the remaining eight teeth (MCZ 64/91 G 3–8, 10) were found in the uppermost Ørsted Dal Member (Tait Bjerg Beds).

Sulej et al. (2014) reported abundant Late Triassic vertebrate material from the Malmros Klint and Ørsted Dal Members of the Fleming Fjord Formation. To date, this material has not been described. Among the most significant vertebrate fossils reported from the 2014 expedition were archosaur bone remains including fragmentary limbs and pelvis associated with dinosauriforms and theropod dinosaurs from Macknight Bjerg, the latter including part of a maxilla, two isolated teeth, two cervical vertebrae, fragmentary tibia, fibula, pubis, ischium, dorsal and caudal vertebrae and tentatively attributed to a coelophysoid theropod (Niedzwiedzki & Sulej 2017). There are also sauropodomorph and theropod dinosaur tracks and trackways from Macknight Bjerg, remains of stem turtles and a potential pterosaur,

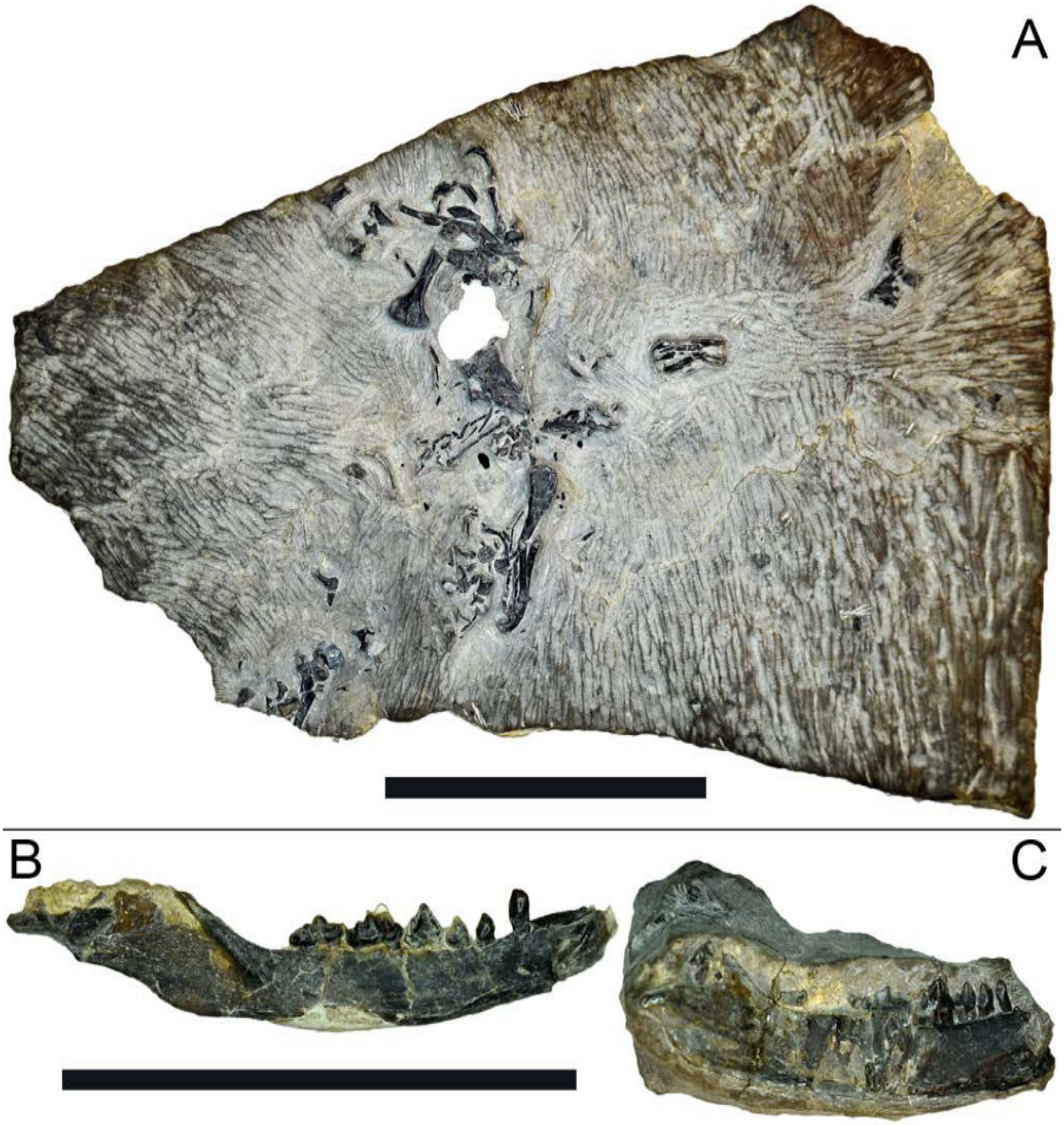

Figure 1.16 - The haramiyid *Haramiyavia clemmenseni* Jenkins et al. 1997, holotype MCZ 7-G95 from the Late Triassic of the Fleming Fjord Formation. A: Main block with cranial and postcranial elements. B: Right mandible in labial view. C: Left mandible in lingual view. Scale bars, A: 5 cm; B and C: 2 cm.

an incomplete mandible and associated dentition of a stem mammal from Liasryggen (Jameson Land) and pentadactyl tracks, possibly of stem mammal affinity.

Trace fossils

***Eosauropus* isp. Lockley et al. 2006a**

Referred specimens. Trackways S1 and S2 described in Lallensack et al. (2017, figs. 2–3).

Locality. ‘Track Mountain’, on a north-east slope of Wood Bjerg–Macknight Bjerg, Jameson Land (Trackway S1: 71°24.853′ N, 22°33.322′ W and 534 m a.s.l.; Trackway S2: 71°24.955′ N, 22°32.952′ W; Fig. 1.1F).

Horizon. Ørsted Dal Member (lowermost Tait Bjerg Beds), Fleming Fjord, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Sulej et al. (2014); Lallensack et al. (2017).

Comments. The Eosauropus trackways described in Lallensack et al. (2017) are the largest tracks known for this morphotype and were potentially made by sauropod dinosaurs; the tracks represent the first evidence of the clade Sauropoda from Greenland and extend their presence back to the Late Triassic.

Evazoum isp. Lockley et al. 2006b

Referred specimens. Trackways S3 as described by Lallensack et al. (2017, fig. 4).

Locality. ‘Track Mountain’, on a north-east slope of Wood Bjerg–Macknight Bjerg, Jameson Land, 71°24.857′ N, 22°33.334′ W (Fig. 1.1F).

Horizon. Ørsted Dal Member (lowermost Tait Bjerg Beds), Fleming Fjord, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Sulej et al. (2014); Lallensack et al. (2017).

Comments. The *Evazoum* trackway described in Lallensack et al. (2017) was made by a bipedal trackmaker, potentially a non-sauropod sauropodomorph dinosaur, and are the largest known tracks ascribed to this morphotype.

Grallator Hitchcock 1858

Referred specimens. MGUH 27811–27915 described by Milàn et al. (2006) and further tracks described by Gatesy et al. (1999, p. 142, fig. 1), Gatesy (2001, p. 139, fig. 1), Milàn et al. (2004, p. 289, fig. 4), and Clemmensen et al. (2016, p. 42, fig. 8).

Locality. Different localities at Tait Bjerg and Wood Bjerg, Jameson Land (Fig. 1.1F).

Horizon. Malmros Klint and Ørsted Dal Member, Fleming Fjord Formation, lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Jenkins et al. (1994); Gatesy et al. (1999); Gatesy (2001); Milàn et al. (2004); Suley et al. (2014); Clemmensen et al. (2016).

Comments. The *Grallator* tracks have an average foot size of 23.5 cm length and 8 cm width; trackways have an average pace of 61 cm and step of 119 cm (Clemmensen et al. 2016). They were attributed to ceratosaurid theropod dinosaurs by Gatesy et al. (1999). The record is extremely rich, including thousands of tracks from multiple horizons in the middle and upper part of the Malmros Klint Member, the overlying Carlsberg Fjord beds (the most abundant source) and the lowermost Tait Bjerg Beds of the Ørsted Dal Member (Milàn et al. 2014; Suley et al. 2014; Clemmensen et al. 2016).

cf. *Brachychirotherium* Beurlen 1950

Referred specimens. MGUH 31233a–c and MGUH 31234, two slabs preserving tracks as concave epireliefs (true tracks); MGUH 31235, a slab bearing tracks as convex hyporeliefs (natural casts).

Locality. Tait Bjerg (MGUH 31235) and north of Lepidopteriselv (MGUH 31233a–c and MGUH 31234, 71°15.687′ N, 22°32.326′ W, 242 m a.s.l.), Jameson Land (Fig. 1.1F).

Figure 1.17 - Early Jurassic plesiosaur from the Kap Stewart Formation of the Jameson land Basin: two vertebrae NHMD 74795 (A–D), NHMD 74756 (E–F) and a rib NHMD 74797 (G–H). A: Dorsal view. B, E, G: Frontal views. C: Lateral right view. D: Lateral left view; F: Ventral view; H: Medial view. Scale bar: 2 cm.

Horizon. Ørsted Dal Member (Carlsberg Fjord beds), Fleming Fjord Formation, fluvial and lacustrine deposits; subtropical arid to winter-wet, warm temperate climate.

Age. Late Triassic (late Norian to early Rhaetian).

Selected bibliography. Klein et al. 2016.

Comments. Klein et al. (2016) attributed these footprints to crocodylomorph archosaurs.

Other tracks Sulej et al. (2014) reported at least nine provisional morphologies among the tracks recovered from different beds of the Fleming Fjord Formation, including cf. *Brachychirotherium* isp., cf. *Apatopus* isp., cf. *Atreipus* isp., *Chirotheriidae* indet., *Grallator* isp., *Eubrontes* isp., cf. *Evazoum* isp., *Eosauropus* isp. and cf. *Tetrasauropus* isp.. Hansen et al. (2016) reported vertebrate coprolites of which many could be of tetrapod origin.

Jurassic

Skeletal fossils

Plesiosauria *indet*. (Diapsida: Sauropterygia)

Referred specimens. Two partial vertebrae NHMD 74795 and NHMD 74796; a partial rib NHMD 74797 (Fig. 1.17).

Locality. East slope of a mountain near Lepidopteriselv, 71°15.761′ N, 22°34.287′ W, 498 m a.s.l., Jameson Land (Fig. 1.1F).

Horizon. Middle part of the Kap Stewart Formation, delta front sheet sandstone; warm temperate humid climate.

Age. Early Jurassic (Hettangian).

Selected bibliography. Milàn et al. (2016b).

Comments. This material was collected during the GeoCenter Møns Klint expedition in the summer of 2016 and comprises small amphicoelous vertebral centra with a diameter of 2 cm that bear paired ventral nutritive foramina and unfused neurocentral sutures. The finds record marine tetrapods in the Kap Stewart Formation prior to the complete transgression in the Pliensbachian (see Dam & Surlyk 1992).

Cryptoclididae *indet*. (Sauropterygia: Plesiosauria)

Referred specimen. MGUH 28378, a partial skeleton consisting of dorsal and cervical vertebrae and ribs, part of scapular girdle, and forelimb (Fig. 1.18).

Locality. East of Milne Land, Scoresby Sund, 70°40.61′ N, 25°22.83′ W (Fig. 1.1E).

Horizon. Krebsedal Member, Kap Leslie Formation, offshore shelf deposits; warm temperate humid climate.

Age. Late Jurassic (Kimmeridgian).

Selected bibliography. von Huene (1935); Bendix- Almgreen (1976); Smith (2007).

Figure 1.18 - The cryptoclidid plesiosaur MGUH VP 28378: partial skeleton from the Kimmeridgian (Late Jurassic) of East Milne Land, Scoresby Sund. Scale bar: 20 cm.

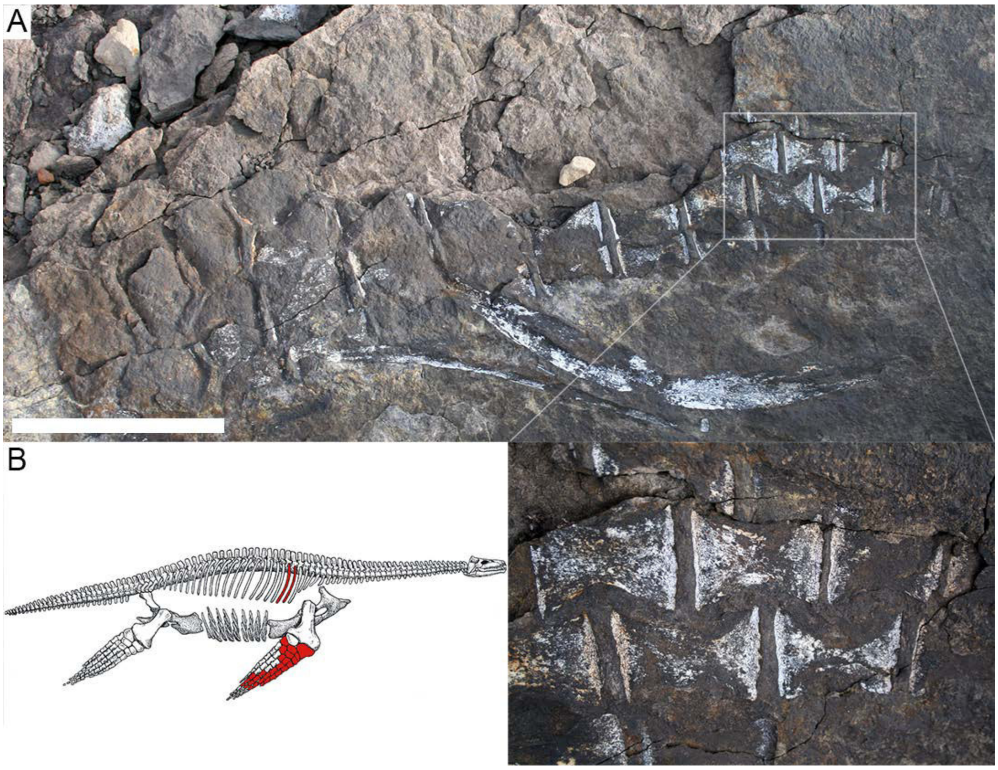

Figure 1.19 - Late Jurassic plesiosaur from Kilen. A: The frontal right paddle as found on the field. B: reconstruction of the surveyed material using *Cryptoclidus* from Andrews (1910) as model. Scale bar in A: 20 cm.

Comments. Originally ascribed to *Cryptoclidus (Apractocleidus) aldingeri* von Huene 1935, this specimen was re-evaluated by Smith (2007) as an indeterminate cryptoclidid.

Plesiosauria *indet*. (Diapsida: Sauropterygia)

Locality. Kilen (near Station Nord), Kronprins Christian Land, 81°15.623′ N, 13°57.007′ W (Fig. 1.1C).

Horizon. Wandel Hav Basin, Kuglelejet Formation. The Kuglelejet Formation comprises a fine- to medium-grained sandstone succession which is sporadically bioturbated (Dypvik et al. 2002).

Age. Late Jurassic (Upper Kimmeridgian/Middle Volgian).

Comments. This specimen was initially discovered in 1998 by a team of Danish and Norwegian geologists exploring for tsunami deposits from a meteor impact in the Barents Sea around the Jurassic–Cretaceous boundary. It has been described briefly by Bruhn (1999) and Dypvik et al. (2002) as "… well preserved skeletal material probably belonging to *Plesiosaurus*". The site was revisited in 2008 by one of us (JM) to evaluate if an excavation would be feasible (Milàn 2009). The original remains consist of impressions of two gastralia and a partial articulated limb (Fig. 1.19).

Ichthyosauria *indet*. (Diapsida: Ichthyopterygia)

Referred specimen. NHMD 74798, includes fragmentary blocks that preserve three vertebrae with ribs and a tooth (Fig. 1.20).

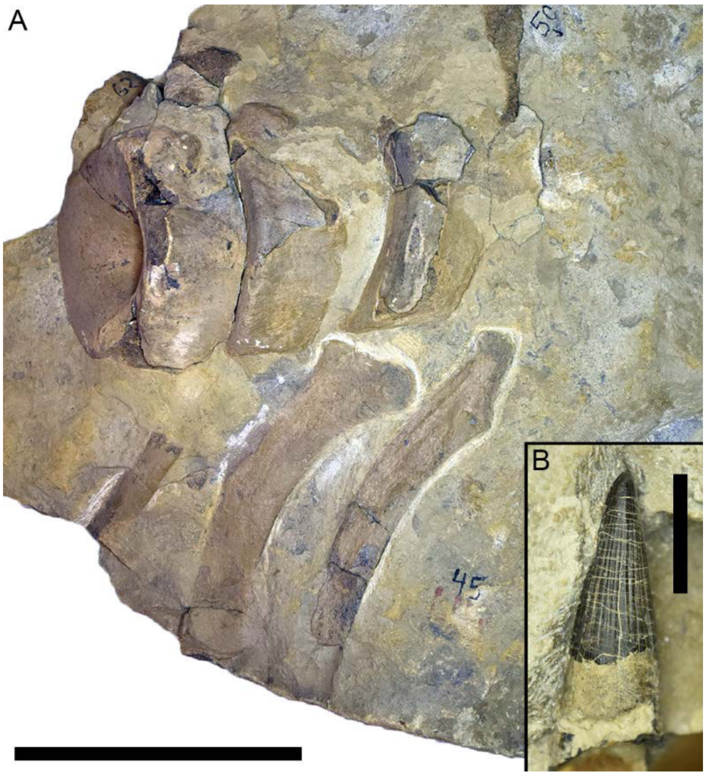

Figure 1.20 - Undetermined ichthyosaur NHMD 74798 from the Upper Kimmeridgian (Late Jurassic) of the Kap Leslie Formation in Milne Land, Scoresbysund. A: Block including three vertebrae and ribs. B: Tooth. Scale bars, A: 10 cm; B: 1 cm.

Locality. Pernaryggen, Milne Land, Scoresbysund, 70°43.033′ N, 25°24.050′ W (Fig. 1.1E).

Horizon. Krebsedal Member, Kap Leslie Formation, offshore shelf deposits; warm temperate humid climate.

Age. Late Jurassic (Upper Kimmeridgian).

Selected bibliography. Håkansson et al. (1971). Comments. This specimen was mentioned by Håkansson et al. (1971) but has never been formally described.

Faunal correlations

The Devonian tetrapod fauna of Greenland is characterised by five endemic stem tetrapod species. Though the phylogeny of Late Devonian stem tetrapods is still ambiguous, the taxa closest to *Acanthostega*, *Ichthyostega*, and *Ymeria* are *Metaxygnathus* Campbell & Bell 1977 from Australia, *Ventastega* Ahlberg et al. 1994 from Latvia, *Densignathus* Daeschler 2000 from USA, *Elginerpeton* Ahlberg 1995 from Scotland, and *Elpistostege* Westoll 1938 and *Tiktaalik* Daeschler et al. 2006 from Canada (see also Ruta et al. 2003; Ruta & Coates 2007; Neenan et al. 2014).

The Early Triassic temnospondyls in the Wordie Creek Group show an affinity to coeval faunas from Central Europe, Russia, and Gondwana. *Aquiloniferus* was originally ascribed to *Lyrocephalus* Wiman 1914, and we consider *Aquiloniferus* as belonging to, or as being very closely related to, the Early Triassic clade of the Lydekkerinidae known from Antarctica, Australia, India, Madagascar, Russia and South Africa (Jeannot et al. 2006). *Selenocara* is known from the Early Triassic of Russia and belongs to the Wetlugasaurinae, a clade distributed in Eastern Europe (Novikov 2016). *Stoschiosaurus* belongs to the clade of the Trematosauridae from the Early Triassic of Europe, Africa, Asia, Australia and North America (Welles 1969, 1993; Damiani et al. 2000; Damiani & Welman 2001; Schoch 2006; Maganuco & Pasini 2009; Warren 2012). *Tupilakosaurus* is recognised from the Early Triassic of Russia, and the clade Tupilakosauridae is recorded in the Early Triassic of Greenland, Russia and South Africa (Shishkin & Novikov 1992; Warren 1998).

Even though Greenland is part of the North American plate, its Late Triassic tetrapod fauna has more affinities with coeval faunas of Europe than to any other areas; among Amphibia, *Cyclotosaurus* Fraas 1889 is restricted to Europe (Germany, Poland, and the Svalbard archipelago), with *C. naraserluki* being the westernmost and northernmost of the known species, endemic to East Greenland (Marzola et al. 2017b). The taxa closest to *Cyclotosaurus* are *Quasicyclotosaurus* Schoch 2000 from the Middle Triassic of Arizona and *Eocyclotosaurus* Ortlam 1970 from the Middle Triassic of Central Europe, UK, Algeria, and southern USA (Arizona and New Mexico) (Schoch 2008; Witzmann et al. 2016). The European origin of the Capitosauria can be pinpointed to Central East Europe, with its most primitive taxon, *Eryosuchus* Ochev 1966 from the Middle Triassic of Russia (Lehman 1971; Lucas & Hunt 1987; Morales 1987; Ochev & Shishkin 1989; Milner et al. 1990; Sulej & Majer 2005; Schoch 2008; Witzmann et al. 2016; Kear et al. 2016b).

The plagiosaurid *Gerrothorax* Nilsson 1934 is reported from the Middle and Late Triassic of Germany and Sweden, with the clade Plagiosauridae recorded throughout the Triassic of Europe, Australia and Brazil (see Bartholomai 1979; Hellrung 2003; Dias-Da-Silva & Ramos Ilha 2009; Witzmann et al. 2012). Among Stagonolepididae, the closest relatives to the Greenlandic *Aetosaurus* are the Late Triassic *Stagonolepis* Agassiz 1844 from Germany, Poland and UK, and *Aetosauroides* Casamiquela 1960 from Argentina and Brazil. The Late Triassic *Paratypothorax* is the only Greenlandic tetrapod taxon with a North American origin: it is documented also from Germany and southern USA, it is closely related to *Rioarribasuchus* Lucas et al. (2006) and *Tecovasuchus* Martz & Small 2006 from the Late Triassic of Arizona, Mexico and Texas (Long & Ballew 1985; Heckert & Lucas 1999, 2000; Schoch 2007).

Among Archosauria, the relationships of the pterosaur *Arcticodactylus* is still under debate; however, recent analyses (Kellner 2015; Upchurch et al. 2015) propose a close relationship to Italian taxa *Carniadactylus* Dalla Vecchia 2009 and *Eudimorphodon* Zambelli 1973. A preliminary analysis of the sauropodomorph dinosaur remains briefly described in Jenkins et al. (1994) allows for the correlation between Greenlandic specimens and Plateosauridae, however differentiating it from *Plateosaurus*. Plateosauridae are recorded from Eurasia and South America (Lapparent 1967; Galton 1986, 2001; Kellner & Campos 2000; Hurum et al. 2006; Klein & Sander 2007; Novas et al. 2010).

Shapiro & Jenkins (2001) proposed that the closest relative to the Greenland cynodont *Mitredon* is Meurthodon Sigogneau-Russell & Hahn (1994) from the Triassic of France. The clade Haramiyidae is distributed throughout the Late Triassic and includes *Haramiyavia* from Greenland, *Theroteinus* Sigogneau-Russell et al. (1986) from France and some undetermined remains from Switzerland (Clemens 1980).

Conclusions

The complete known Palaeozoic and Mesozoic tetrapod fossil record of Greenland includes at least 30 taxa, comprising the Late Devonian stem tetrapods *Acanthostega gunnari*, *Ichthyostega eigili*, *I. stensioi*, *I. watsoni* and *Ymeria denticulate*; the Early Triassic temnospondyls *Aquiloniferus kochi*, *Selenocara groenlandica*, *Stoschiosaurus nielseni* and Tupilakosaurus heilmani; the Late Triassic temnospondyls *Cyclotosaurus naraserluki* and *Gerrothorax* cf. *pulcherrimus*, the stagonolepids *Aetosaurus ferratus* and *Paratypothorax andressorum*, the eudimorphodontid *Arcticodactylus*, the cynodont *Mitredon cromptoni* and the three mammals *Haramiyavia clemmenseni*, *Kuehneotherium* and cf. ?*Brachyzostrodon*. Undetermined remains are represented by Late Triassic testudinatans, archosaurs (such as phytosaurs and both sauropodomorph and theropod dinosaurs), and Early and Late Jurassic plesiosaurs and ichthyosaurs. Fossil tracks associated to tetrapod trackmakers are reported from the Late Carboniferous (eryopoid temnospondyls morphotype *Limnopus*) and from the Late Triassic (crocodylomorph morphotype *Brachychirotherium*, sauropodomorph morphotypes *Eosauropus* and

Evazoum, and theropodian morphotype *Grallator*). Tetrapod coprolites have also been found from the Jameson Land Basin. The two most productive stratigraphical sections are the Devonian, with five recorded taxa and as many unique species, and the Triassic, with 18 recorded taxa and at least eight endemic species.

The richness and diversity of Late Devonian and Triassic tetrapods is due to the formation of terrestrial deposits and their later preservation and exposure during uplift. Through both the Late Devonian and the Triassic, East Greenland was characterised by extensional subsidence, followed by rapid filling of the resulting basins. These events can be linked to the Caledonian crustal welt collapse during the Middle to Late Devonian and the various Triassic rifting phases during the initial breakup of Pangaea (Larsen et al. 2008; Clemmensen 1980a, b; Nøttvedt et al. 2008). Synrift sediment deposition and subsequent preservation of vertebrate fossils are well documented worldwide during different epochs and contributed to the existence of fossil vertebrate lagerstätten (Hallam 1971; Feibel et al. 1989; Clemmensen et al. 1998; Mateus 2006; Larsen et al. 2008; Wood & Leakey 2011). Further studies will clarify the phylogenic position of the yet poorly reported tetrapod material from Greenland, focusing on the origin of the Late Triassic biota of the Jameson Land Basin and on the different influences of climate and geography on the distribution of life on Earth during the Late Triassic.

Addendum on the Phytosauria and Sauropodomoprha material - Unpublished

Phytosauria material has been allegedly recovered from East Greenalnd during the Harvard-Danish expeditions to the Jameson Land Basin in 1989 (field nº G/15/89, *"?phytosaur, weathered & fragmented"*; see A6); 1991 (field nº 65/91G, *"Reptile jaw fragment, ?plesiosaur ?phytosaur"*; see A7), and 1995 (field nº 6/G95,*"Phytosaur skull and mandibles"*; see A8) (A5–A11). However, this material not only remains unstudied, but even the most promising specimen (the 1995 skull with mandibles) remains today unknown and unfound among the material given for this PhD project. Hence, the phytosaur bones recovered during the two expeditions in 2012 and 2016 are here considered the first unequivocal reports and remains of phytosaurs from the Late Triassic of Greenland. At least six indivi duals (four adults, one subadult, and a juvenile) and are here properly attributed to every individual, such as: NHMD 74733, adult (partial skull and postcranial bones, Fig. 3.11D); NHMD 74734, adult (left humerus); NHMD 74735 sub-adult (distal left snout); NHMD 74736, juvenile (a left distal snout and left humerus). In addition, two new phytosaur specimens are here reported as two adult individuals: the left humerus NHMD 300676 (field nº 6F-12-62) and the left humerus NHMD 300677 (field nº 6F-13-105), both found during the expedition in 2016 (see Marzola et al. 2017a). Among this material, at least fourteen specimens have been photogrametrized (Table 1.1, S1.1– S1.14).

Table 7.2 - List of the photogrammetrized sauropodomorph specimens from Greenland

Body region	Bone	Field nº	Depository nº	Supplementary Material nº
Cranium	Mandible, left distal	Hc1	NHMD 74733	S1.1
	Mandible, left proximal	Hc4		S1.2
	Snout, right distal	126a	NHMD 74735	S1.3
Axial	Caudal vertebra	132	NHMD 74733	S1.4
	Cervical vertebra	Hc112		S1.5
Forelimbs	Humerus, left	Fa85	NHMD 74733	S1.6
	Humerus, righ	Gc6		S1.7
	Radius, left	133		S1.8
	Ulna, left	Jd57		S1.9
	Humerus, left	Ga116	NHMD 74734	S1.10
	Humerus, left	6F-12-62	NHMD 300676	S1.11
	Humerus, left	6F-13-105	NHMD 300677	S1.12
Hindlimbs	Femur, left	134	NHMD 164734	S1.13
	Tibia, left	Hc47a		S1.14

Numerous remains of Late Triassic basal Sauropodomorpha have been collected since the late 1980's at the Fleming Fjord Formation of the Jameson Land Basin from Harvard expeditions, led by late Prof. Farish A. Jenkins (1940–2012) and from a 2012 Danish expedition, and now are at the GeoCenter Møns Klint in Denmark (see Marzola et al. 2018; see also A5–A11 for complete field reports from Harvard-Denmark expeditions). To our knowledge, there is at least one complete adult individual in exhibition and more prepared material lying in crates at the museum storage. Aside the adult skull briefly reported in Jenkins et al. (1994), all the above-mentioned material is unreported in official publication. A brief inspection of these crates in June 2017, allowed us to find pristine sauropodomorph bones, allegedly a juvenile, including a complete skull, vertebrae, limb bones, and a complete hand. By field reports of Harvard's expeditions and by direct observation, we know that more of the juvenile specimen is present in the crates and yet to be unpacked. The entire sauropodomorph material from Greenland, to our knowledge includes, so far, a skull of an adult (Jenkins et al. 1994), a second complete adult (in exhibition such as for August 2017; Fig. 1.13E) and cranial and postcranial material from a subadult juvenile (in the crates at GeoCenter Møns Klint storage). At least thirty sauropodomorph bones from the Late Triassic of Greenland have been photogrametrized (Table 1.2, S1.15– S1.41).

However, to-date, none proper study on the anatomy and the morphology of these Greenlandic taxa has been made. The sauropodomorphs from Greenland have been attributed to *Plateosaurus engelhardti*, though our preliminary analysis leads to a potential new taxon within the Plateosauria clade. The most of these taxa is currently preserved and exposed at the GeoCenter Møns Klint (Denmark), but sooner or later it will be given back to Greenland, for they belong to its paleontological heritage.

Body region	Bone	Depository nº	Supplementary Material nº
Cranium	Skull, upper part	NHMD 164734	S1.15
	Mandible, right proximal		S1.16
	Mandible, left proximal		S1.17
	Mandibles, distal right & left		S1.18
	Skull, upper and lower	NHMD 164758	S1.19
	Skull, upper and lower	NHMD 164775	S1.20
Cranium + Axial	Braincase + atlas & axis	NHMD 164734	S1.21
Axial	Cervical 8	NHMD 164734	S1.22
	Dorsal vertebrae 1–2		S1.23
	Sacrum		S1.24
	Tail, partial (nine caudals)		S1.25
Girdles	Ilium, left	NHMD 164734	S1.26
	Ilium, right		S1.27
	Pubis, right		S1.28
	Scapulacoracoid, left		S1.29
Forelimbs	Humerus, distal left	NHMD 164734	S1.30
	Humerus, proximal left		S1.31
	Manus, left		S1.32
	Manus, right		S1.33
Hindlimbs	Astragalus, right	NHMD 164734	S1.34
	Digit II, right		S1.35
	Digits III-IV, right		S1.36
	Femur, right		S1.37
	Metatarsal I, left		S1.38
	Metatarsal V, right		S1.39
	Tibia, right		S1.40
	Ungual		S1.41

Preliminary results on the phytosaur material - Unpublished

Cranial

Considering size ranges and duplication of bones, the phytosaur material from this quarry pertain to at least to six individuals and three size ranges. Most bones are an adult individual with an estimated size of about 3.8 m long (NHMD 74733; Fig. 7.1). This estimation was conducted based on the illustration by Stocker and Butler (2012: fig 3A), with the postcranial scaled up 30% to the skull to fit the Greenland specimen for life-size reconstruction made for exhibition at the GeoCenter Møns Klint.

The cranial material includes a right jugal (field nº Hc87 - adult), a left quadrate (Hc47b - adult), a left postorbital (Jc72 - adult) a left lower jaw (Hc1, Hc4, and Jd53 - adult), a left lower jaw (126a and Gb95c - subadult), a lower distal jaw (Gb8 - juvenile), and numerous teeth. The jugal is complete except for the ascending process and the posteroventral section. The bone is ornamented, mainly in the anteroventral part. The main body is more than three times longer (98 mm) than high (24 mm). The lower rim is concave, curving gently, such as in *Machaeroprosopus gregorii* Camp 1930. The maxilla attaches anteroventrally in ascending slope such as in *Mystriosuchus westphali* Hungerbühler and Hunt 2000, but clearly not extending anteriorly as in *Parasuchus hislopi* Lydekker 1885. The participation in the antorbital fenestra is not visible but if there is any contribution is minimal. The main body is rectangular, without expanding dorsoventrally toward the posterior end as in *Leptosuchus crosbiensis* Case 1922 and similar to *M. gregorii*. The postorbital contacts with the parietal medially, with the prefrontal anteriorly, with the lacrimal at the ventrolaterally end of the descending process, and with the squamosal posteriorly. Also, it has a significant contribution to the orbit, supra and infratemporal openings. The lacrimal process of the postorbital is narrow being about one third in comparison to the postorbital body in dorsal view. In the left postorbital, the squamosal process is quite broad, and ends quite bluntly, not tapering, and looking more derived, not basal like in *Paleorhinus* and *Parasuchus*.

The lower jaw is nearly complete, except for the ventral part of the middle third, being 670 mm long. The outline resembles *Machaeroprosopus* and *Smilosuchus adamanensis* Camp 1930, such as the minute teeth, the sub-horizontal surrangular, a dorsoventrally compressed dentary, and a short posterior part of the jaw (distance between the last tooth and the articular is less than one third of the jaw length).

The 49 cm long left dentary holds 43 round tooth alveoli. Four teeth are in situ in dentary alveoli position 3, 4,11, and 36. The alveoli are round in outline and become sub-rectangular in the posterior positions. The teeth size vary as follows: the three first teeth form a rosette in which the second tooth is the largest (12 mm in diameter), the fourth tooth is the smallest (4 mm) of whole series, but teeth gradually increase in size posteriorly, with a rapid increase at the 29th to the 32nd position. The symphysis extended to the 29th tooth position, occupying the anterior 27 cm of the dentary. The lateral surface bears two parallel horizontal grooves about 6 mm apart, being the dorsal groove about 2 mm wide, and with nutrition foramina and the ventral groove a narrow furrow about 0.5 mm width. The dentary teeth are different according to the position. Only the teeth 3, 4, 11, and 36 are present in situ but a few isolated teeth were also recovered. The teeth 3, 4 and 11 (symphiseal teeth) are small, round in cross-section, recurved medially, with no carina or serration. The tooth in the 36th position is much larger, D-shaped in crown cross-section and ellipsoid near the root. The anterior and posterior carinae bear well visible serration. It is only slightly recurved lingually. The proximal juvenile right dentary (Gb8) presents with nine alveoli is only of 60 mm, while in the adult the same nine first alveoli are 91 mm. In comparison, the juvenile has a much more robust dentary.

Postcranial

The juvenile cervical vertebra neural arch Eb9b is very similar to cervical vertebra 4 or 5 of *Angistorhinus grandis* Mehl 1913 (see Lucas et al. 2002, Fig. 3), except the fact the transverse process is positioned in a slightly more ventrally. The neural central suture is not fused so the centrum is absent. The neural spine is more than half the height of this section. The neural spines of the caudal vertebrae are not transversely expanded such as in *Machaeroprosopus* and *S. adamanensis*.

The right coracoid Hc75a is 175 mm long and 130 mm deep. It a thin and blade-like except to the expanded glenoid area. The glenoid and facet for the scapula are well separated from the coracoid blade by a neck form and anterior and posterior notches thus the coracoid foramen is absent. The glenoid 136 has a general outline very similar to *Rutiodon carolinensis* Emmons 1856. Fa82 in the anterior portion of the interclavicle, so maybe fits with the other interclavicle Fb31. The interclavicle is 229 mm long, with the anterior section missing, so the total estimated length is about 30-33 cm. Interclavicle is an unpaired bone, nearly transversely expanded blade-like. convex ventrally and concave dorsally.

Five humeri (four left and one right side) of comparable size were collected in the same fossil quarry. The Greenland specimens are hourglass-shaped, with wide ends and narrow epiphysis, such as in humerus of *Paleorhinus arenaceus* ZPAL AbIII 1516 and *Pseudopalatus buceros* NMMNH P-20852 (see Kimming 2016, Fig. 5). There is a concavity in the proximal end between the proximal-lateral corner and humeral head. The distal tuberculae are much more pronounced in the Greenland specimen, when compared *to Nicrosaurus kapfii*. Also, *N. kapfii* has a very round proximal end and more stout diaphysis. The general outline is favorably compared to *Machaeroprosopus pristinus* UCMP 121966 (Stocker & Butler 2013, fig. 4): bowed medially, straight laterally, three-prominent tuberosities proximally, and conspicuous deltopectoral crest. The disto-medial corner of the distal end makes a 90° angle with the distal end (in anterior or posterior views) providing a vertical lateral facet (i.e., subparallel to the shaft), and the rugosity extends into a more proximal level than the ulnar condyle, a potential diagnostic character. The ulnar condyle is much more expanded anteroposteriorly and dorsally, than the radial condyle.

CHAPTER 2 - *CERATODUS TUNUENSIS*, SP. NOV., A NEW LUNGFISH (SARCOPTERYGII, DIPNOI) FROM THE UPPER TRIASSIC OF CENTRAL EAST GREENLAND

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Abstract

The fossil record of post-Paleozoic lungfishes in Greenland is currently restricted to a few brief reports of isolated and undetermined tooth plates coming from the uppermost Fleming Fjord Formation (late Norian) in Jameson Land, central East Greenland. Here, we describe *Ceratodus tunuensis*, sp. nov., a new dipnoan from a thin bed of calcareous lake mudstone from the Ørsted Dal Member of the Fleming Fjord Formation. The *Ceratodus* fossil record indicates that during the Late Triassic, this genus was restricted to the middle latitudes of the Northern Hemisphere. This record matches previous paleobiogeographical analyses and indicates that terrestrial biota during the Late Triassic was strongly influenced by paleolatitude.

Introduction

Lungfishes have a very long evolutionary history. The oldest fossil record of Dipnoi is Devonian (see Long 2011) but finds become notably abundant in post-Paleozoic deposits (Martin 1982; Schultze 2004). Living forms are represented by three genera in South America, Africa, and Australia (Nelson et al. 2016).

Fossil lungfish tooth plates are only relatively common in Upper Triassic rocks from Europe (Schultze 2004). Apart from that, European dipnoans still have a patchy fossil record. Several genera of dipnoans have been described from the Upper Devonian of East Greenland (Lehman 1959; Bendix-Almgreen 1976), but so far the only post-Paleozoic reports of dipnoans have been restricted to brief mentions of isolated tooth plates coming from the uppermost Fleming Fjord Formation (late Norian) in Jameson Land (Jenkins et al. 1994; Clemmensen et al. 1998, 2016).

Here, we describe tooth plates and jaw bones belonging to *Ceratodus tunuensis*, sp. nov., a new lungfish taxon from the uppermost Fleming Fjord Formation. As the first post-Paleozoic record of fossil lungfishes from Greenland, these specimens add valuable information on the genus *Ceratodus*.

Materials and Methods

Geological Setting

During the Triassic, what is now East Greenland was located at the northern rim of the Pangaean supercontinent at about 40N and bounded to the north by the Boreal Sea (Nøttvedt et al. 2008; Clemmensen et al. 2016). Triassic sediments are well exposed in the Jameson Land Basin, located in central East Greenland at about 71N in the present-day land areas of Jameson Land and Scoresby Land (Fig. 2.1).

The thickness of the Triassic succession in East Greenland varies between 1.0 and 1.7 km (Nøttvedt et al. 2008). At the beginning of the Triassic, the Jameson Land Basin is interpreted as a marine bay (Boreal Sea), which gradually underwent regression and continental emergence up through the Early Triassic (Clemmensen 1980a, 1980b; Nøttvedt et al. 2008). These overlying sediments are

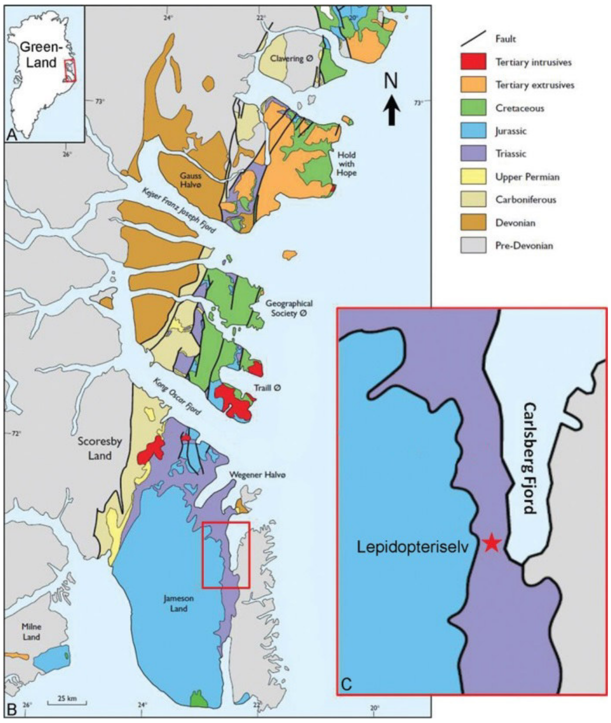

Figure 2.1 - Location map of the East Greenland showing the Mesozoic deposits in the Jameson Land Basin. A, small insert showing Greenland, with East Greenland indicated by the box. B, geological map of East Greenland, with the Carlsberg Fjord locality indicated by the box. C, close-up of the eastern part of the basin near Carlsberg Fjord and the locality with Upper Triassic rocks at Lepidopteriselv. Modified from Stemmerik et al. (1997).

continental and comprise alluvial fan, river, aeolian dune, saline lake, and freshwater lake deposits (Clemmensen 1980a; Clemmensen et al. 1998). The prominent freshwater lake deposits from the uppermost part of the Triassic succession (the Fleming Fjord Formation) are particularly well exposed in cliff sides facing the Carlsberg Fjord (Fig. 2.2). The Fleming Fjord Formation is of Norian–early Rhaetian age, and the fossil-bearing layer in the Carlsberg Ford beds has a likely age of about 208 Ma (see Clemmensen et al. 1998).

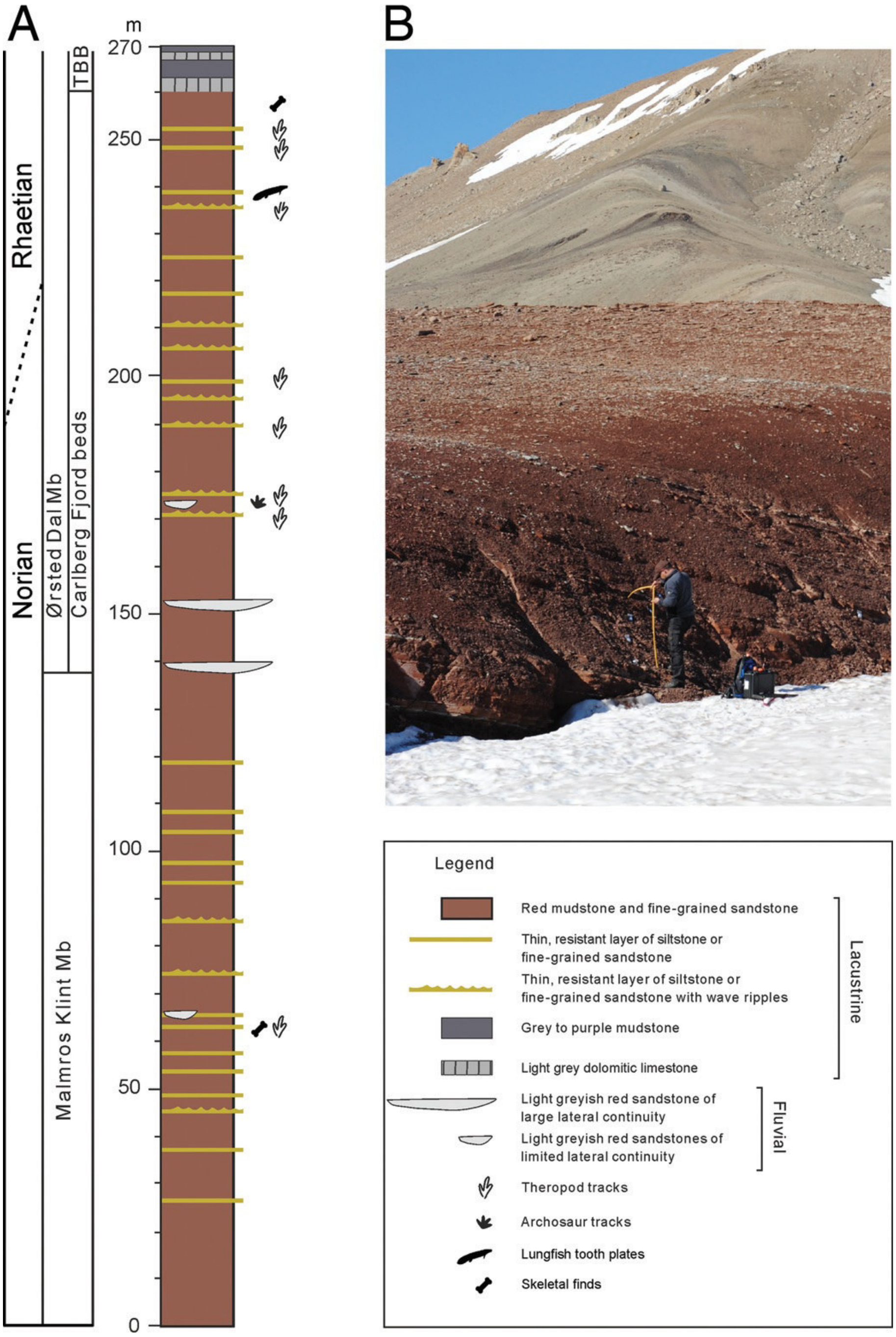

Figure 2.2 - A, stratigraphic scheme of the Triassic succession exposed at Carlsberg Fjord. B, field photo showing the reddish-brown bedded lacustrine sediments of the Ørsted Dal Member.

The new finds of fossil lungfish remains are froma thin (0.1–0.5 m thick) calcareous mudstone bed in the Carlsberg Fjord beds of the Ørsted Dal Member from the uppermost part of the Fleming Fjord Formation (Jenkins et al. 1994; Clemmensen et al. 1998, 2016). The calcareous mudstone bed formed in an ephemeral to semiperennial lake. The lungfish remains are associated with numerous freshwater bivalves, undetermined amphibian remains, and fragments of testudinatans.

Eight specimens were collected during the GeoCenter Møns Klint Dinosaur Expeditions in 2012 and 2016 and are deposited in the NHMD under institutional numbers 115910 to 115917.

Terminology

In the present article, we follow the terminology of Churcher et al. (2006; see also Churcher and De Iuliis 2001) for the tooth plates, and that of Martin (1981) for jaw-bone structures. Distinction between upper and lower tooth plates follows the criteria detailed by Martin (1980, 1981). The angle between the medial and lingual margins of the tooth plate is termed 'inner angle' following Vorobyeva and Minikh (1968). Histological terminology follows Kemp (2001). Measurements were taken as in Apesteguía et al. (2007).

Systematic Paleontology

DIPNOI Müller, 1845
CERATODONTIDAE Gill, 1873
CERATODUS Agassiz, 1838
CERATODUS TUNUENSIS, sp. nov.
(Figs. 2.3–2.5)

Holotype—NHMD 115910, a right upper tooth plate lacking the labial half of the first ridge (Fig. 2.3A).

Referred Material—NHMD 11911, an upper left tooth plate with incomplete mesial margin and first ridge (Fig. 2.3B); NHMD 115912, an upper left tooth plate (Fig. 2.3C); NHMD 115913, a fragmentary left lower tooth plate (Fig. 2.3D); NHMD 115914, an incomplete left lower tooth plate (Fig. 2.4A); NHMD 115915, an incomplete left lower tooth plate (Fig. 2.4B); NHMD 115916, an incomplete left lower tooth plate (Fig. 2.4C); NHMD 115917, a right nearly complete jaw bone including the last ridge of the corresponding tooth plate (Fig. 2.5).

Type Locality—The specimens were collected during the 1990s American-Danish expeditions as well as later by the expeditions conducted by the Geocenter Møns Klint Dinosaur Expeditions to Lepidopteriselv at the eastern margin of the Jameson Land Basin (71°15.7910N, 22°32.6140W and 71°15.6290N, 22°32.7370W).

Type Horizon—Thin calcareous mudstone layer in the late Norian Carlsberg Fjord beds of the Ørsted Dal Member in the Fleming Fjord Formation (Fig. 2.2).

Etymology—The specific name *tunuensis* is from 'Tunu,' the Inuit word for East Greenland.

Diagnosis—Robust dipnoan diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk*): (1) five ridges on upper tooth plates and four ridges

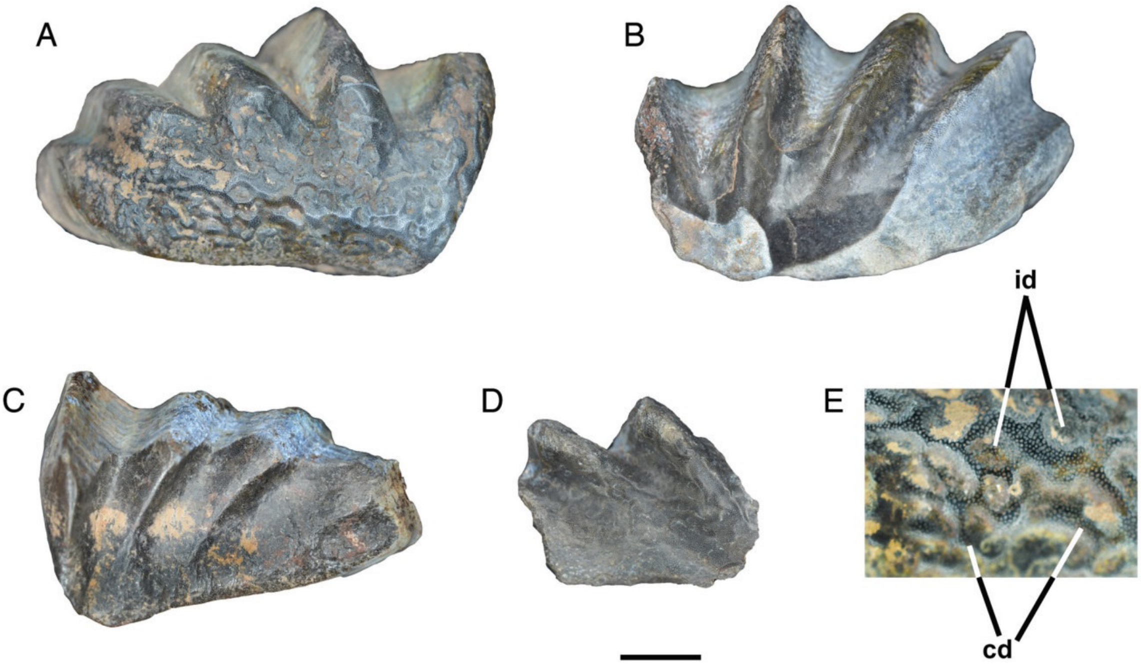

Figure 2.3 - *Ceratodus tunuensis*, sp. nov., holotype and referred material. A, E, holotype NHMD 115910, a right upper tooth plate (A), with details of the tooth plate occlusal surface (E); B, NHMD 115911, an upper left tooth plate; C, NHMD 115912, an upper left tooth plate; D, NHMD 115913, fragmentary left lower tooth plate. Abbreviations: **cd**, circumdenteonal dentine; **id**, interdenteonal dentine. Scale bar equals 1 cm.

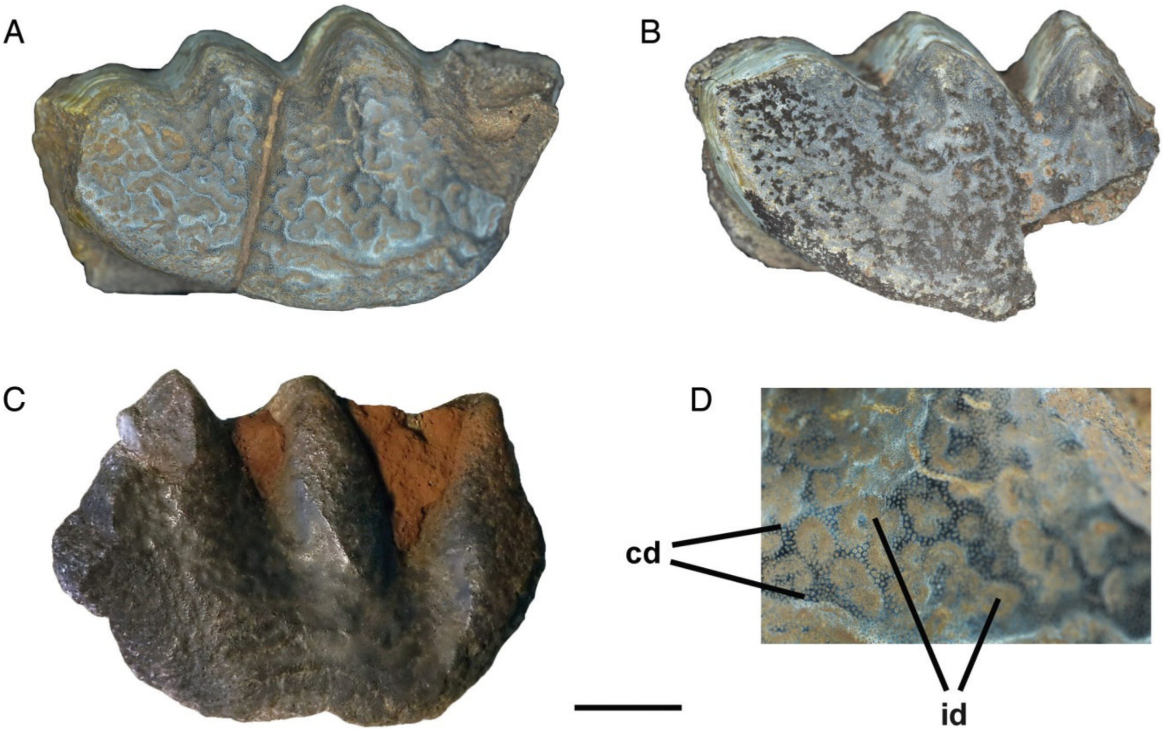

Figure 2.4 - *Ceratodus tunuensis*, sp. nov., referred material. A, NHMD 115914, an incomplete left lower tooth plate; B, NHMD 115915, an incomplete left lower tooth plate; C, D, NHMD 115916, an incomplete left lower tooth plate (C), with details of tooth plate occlusal surface (D). Abbreviations: **cd**, circumdenteonal dentine; **id**, interdenteonal dentine. Scale bar equals 1 cm.

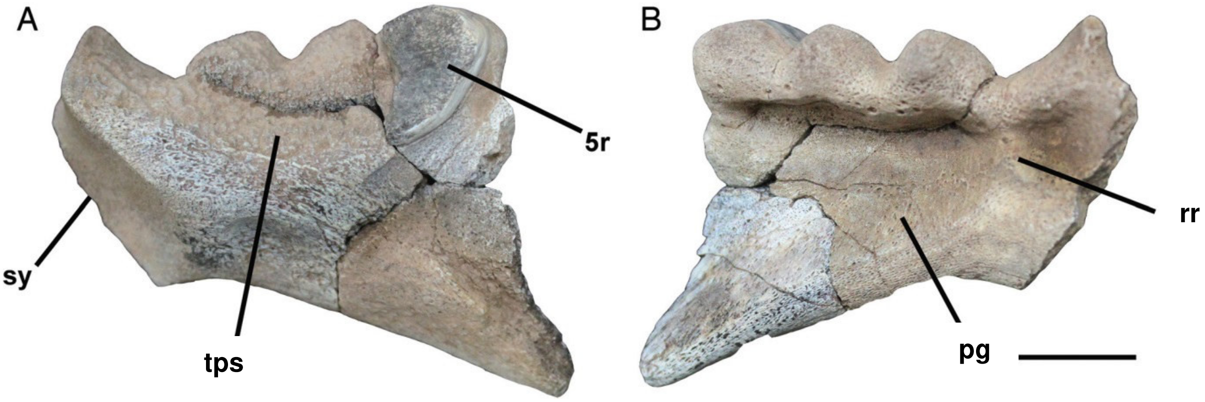

Figure 2.5 - *Ceratodus tunuensis*, sp. nov., referred material, NHMD 115917, right lower jaw bone. A, lateral and B, medial views. Abbreviations: **pg**, prearticular groove; **rr**, Ruge's ridge; **sy**, symphysis of jaw bone; **tps**, tooth plate scar; **5r**, fifth ridge. Scale bar equals 2 cm.

on lower tooth plates; (2) relatively short crests that are separated by wide and shallow inter-ridge furrows; (3) upper tooth plates with well-developed mesiointernal angle; (4) lower tooth plates with lingual margin uniformly convex*; (5) upper tooth plates with straight to slightly concave lingual margin; (6) first ridge of upper tooth plates subequal in size to other ridges; and (7) occlusal surface of the tooth plates with wide and deep occlusal pits that are randomly distributed along most of the tooth plate.

Description

The new species is represented by jaw bones and both upper and lower tooth plates. The specimens are considered as belonging to the same species based on similar size and shape, similar robustness, and coincidence in most features, including presence of irregular occlusal pits along the crushing surface (Table 2.1). Based on the relative stages of wear defined by Martin (1980), none of the plates belong to juvenile or senile individuals.

Upper Tooth Plates

The upper tooth plates are relatively robust and high-crowned. They are roughly subtriangular in contour, being mesiodistally elongate. The ridges are relatively short and robust, with a flat and wide occlusal surface. The ridges are separated by wide and shallow inter-ridge furrows. The inner angle is about 95° in upper tooth plates. The occlusal surface of the plates is very wide and broad, and slightly concave. The whole occlusal surface shows abundant, wide, and irregular occlusal pits that result in a roughly reticulate pattern. Interdenteonal and circumdenteonal dentine are not arranged in an ordered pattern. The plate surface is covered by randomly situated punctuations corresponding to pulp canals (Bemis and Northcutt 1992) of dentine. There is no trace of hypermineralized dentine free of denteons or petrodentine (Kemp 2001). The upper tooth plates have five acute ridges, showing low and wide crests along each ridge. The ridges converge at the mesiointernal angle and do not originate anteriorly

Table 2.1 - Measurements (in mm) of selected specimens of *Ceratodus tunuensis*, sp. nov.

Dimension	NHMD 115910	NHMD 11911	NHMD 115912	NHMD 115914
Total length of the tooth plate	65.2	75	59	54
Total length of first ridge	-	-	37	-
Total length of second ridge	35	33	34	36
Total length of third ridge	33	32	33	34
Total length of fourth ridge	34	-	54	-
Total length of fifth ridge	20	-	-	-
Length of lingual margin	52	-	-	-

as in several neoceratodontids (sensu Kemp 1997). The ridges are relatively straight, and the first ridge is only slightly posteriorly curved and has a nearly straight mesiobuccal margin. The fifth ridge is robust and is not twinned. Ridge size is as follows: 1 > 2 > 4 > 3 > 5. The mesiointernal angle is pronounced, being represented by a relatively well-developed bump. It is located at the level of the second ridge. Denticulations cannot be observed in the buccal margin of the crests. Inter-ridge furrows are relatively shallow and wide, with a rounded lingual end. The first furrow is as deep and wide as the other furrows. The mesiobucal margin of the plate is convex and lacks any sign of contact with the opposite tooth plate.

Lower Tooth Plates

The lower tooth plates have four robust ridges, showing low crests along at the buccal half of each ridge. The inner angle is about 100º in lower tooth plates. The ridges converge at the mesiointernal angle of the plate. The first ridge is not preserved in any specimen. However, the scar left on the jaw bones indicates that this ridge was large, robust, and with a uniformly convex mesiobuccal margin. The fourth ridge is robust and is not twinned. Ridge size is as follows: 1 > 4 > 2 > 3. A mesiointernal keel is absent. The mesial and lingual margins form a continuous convex margin. Denticulations are not observed in the buccal margin of the crests. Inter-ridge furrows are relatively shallow and wide, with a narrow lingual end. The first furrow is subequal in size and shape to the remaining furrows.

The prearticular bone is massive, wide, and robust, being notably anteroposteriorly shortened. It expands transversely in its posterior part. The tooth plate is fully attached to the bone. Due to the long symphyseal process of the prearticular, the tooth plates are separated from each other. The articular surface of the symphysis is decorated by upright minute grooves and ridges. The symphysis is notably dorsoventrally low and buccolingually extended, forming a linear-type symphysis as defined by Kemp (1998). The orientation of the symphysis indicates a relatively wide jaw arcade. There is a deep and wide prearticular groove on the medial surface of the bone. The groove is double, being subdivided subvertically by a relatively shallow Ruge’s ridge. It is located at the level of the first inter-ridge furrow.

Discussion

Post-Paleozoic dipnoans bear prominent masticatory structures known as tooth plates. Due to their high fossilization potential, tooth plates are usually the only known elements of Mesozoic and Tertiary fossil dipnoans (Martin 1982; Cavin et al. 2007; Skrzycki 2015). In most cases, isolated tooth plates show enough features to allow determination at the species level and even might help to infer phylogenetic relationships (see also Cione and Gouiric-Cavalli 2012; Skrzycki 2015; Fanti et al. 2016).

Having relatively robust and thick crushing upper tooth plates with five or fewer ridges lacking tubercles, a convex lingual margin, and prearticular bone with a Ruge's ridge distinguishes *C. tunuensis* from all known pre-Triassic dipnoans (Martin 1982, 1984; Apesteguía et al. 2007). Among ceratodontiforms, presence of five or fewer ridges on upper tooth plates is a feature exclusively shared by species of Ceratodontidae or Ptychoceratodontidae (Martin 1982, 1984; Cavin et al. 2007).

The plates here described are referred to *Ceratodus* on the basis of robust and short ridges having a broad crushing occlusal surface with rounded contours (Martin 1984; Schultze 1991; Kemp 1993; Cavin et al. 2007). This contrasts with the more elongate and acute ridges that are typical of ptychoceratodontids (sensu Martin 1982; see also Skrzycki 2015). Further, in contrast to ptychoceratodontids, including the well-known species *Ptychoceratodus roemeri* and *P. serratus*, the occlusal pits in *C. tunuensis* are abundant over all of the occlusal surface and are not restricted to the inter-ridge furrows (Skrzycki 2015).

Since the 19th century, isolated tooth plates mostly have been referred to the genus *Ceratodus*. However, these plates belong to a large number of genera, as demonstrated by Martin (1980, 1981, 1982, 1984; see also Martin et al. 1981). Analyses of abundant tooth plates by Martin (1980, 1982) resulted in the recognition of only two valid Triassic species referable to *Ceratodus* (*C. latissimus* and *C. kaupi*). Kemp (1993) described a third valid species, *C. diutinus*, from the Cretaceous of Australia. Although some authors have employed *Ceratodus* as a 'form genus' (e.g., Kirkland 1988), as demonstrated by Kemp (1993, 1998), these taxa are not particularly similar to *C. latissimus* Agassiz, 1838, the type species of the genus (see also Pardo et al. 2010; Frederickson and Cifelli 2016).

Taking into consideration the detailed analysis of ontogenetic and intraspecific variation of dipnoan tooth plates carried out by Skrzycki (2015), we noted some features that distinguish *C. tunuensis*, sp. nov., from other species of the genus *Ceratodus*.

Ceratodus tunuensis, sp. nov., differs from *C. kaupi* and *C. diutinus* by the different occlusal contour of upper tooth plates. In the latter two species, the profile of the tooth plates is very broad and relatively mesiodistally short, with a very deep lingual keel, a combination of traits absents in *C. tunuensis*, sp. nov.

On the other hand, the occlusal profile of the tooth plates of *C. tunuensis*, sp. nov., matches that of *C. latissimus* (Kemp 1993). Further, in both *C. tunuensis*, sp. nov., and *C. latissimus*, the occlusal pits are abundant over all of the occlusal surface and are not mainly restricted to inter-ridge furrows as in *C. kaupi* and *C. diutinus* (Kemp 1993). In spite of such similarities, *C. tunuensis*, sp. nov., differs from *C. latissimus* in several important details. In *C. tunuensis*, sp. nov., the first ridge is short and robust, contrasting with the elongate condition exhibited by *C. latissimus* (Miall, 1878). In *C. tunuensis*, sp. nov., the upper tooth plate shows a pronounced mesiointernal angle, whereas in *C. latissimus* such an angle is absent (Kemp 1993). Further, in *C. tunuensis*, sp. nov., lower tooth plates show a uniformly convex lingual margin, lacking any sign of the mesiointernal keel present in *C. latissimus* (Kemp 1993).

The available information suggests that *C. tunuensis*, sp. nov., is a new lungfish species that belongs to the genus *Ceratodus* sensu stricto.

Paleoecological and Paleobiogeographical Implications

Ceratodus tunuensis, sp. nov., was found in rocks of the uppermost Fleming Fjord Formation, which is exclusively lacustrinefluvial in origin (Clemmensen et al. 1998) and lacks any sign of marine influence. Cavin et al. (2007; see also Fernandez et al. 1973; Kirkland 1988) proposed that most, if not all, post-Paleozoic dipnoans were adapted to freshwater habitats (contra Schultze 1991), a fact supported by the depositional origins of most known post-Triassic fossils.

The presence of *Ceratodus tunuensis*, sp. nov., in the Late Triassic (late Norian) of East Greenland constitutes an important addition to the geographical distribution of the genus *Ceratodus*. Late Triassic specimens unambiguously referable to *Ceratodus* are restricted to the Northern Hemisphere (Martin 1982), and no pre-Cretaceous record of this genus is known in the Southern Hemisphere (see Kemp 1993, 1997). From younger deposits, in the Upper Cretaceous and lower Paleogene, species referable to *Ceratodus* have been reported from Australia and South America (Kemp 1993; Agnolin 2010).

Ezcurra (2010) proposed, on the basis of the record of tetrapods, that by the Late Triassic, the geographical distribution of fauna was strongly paleolatitudinally influenced, with several tetrapod lineages restricted to well-defined paleolatitudinal belts. On the basis of the currently known fossil record, it is possible to infer that by the Late Triassic, dipnoans of the genus *Ceratodus* were restricted to middle latitudes. By the Cretaceous, species of the genus *Ceratodus* are totally absent from Europe (Schultze 2004), suggesting local extinction of the genus.

By the Late Cretaceous, the genus *Ceratodus* is found in the Southern Hemisphere, suggesting a very late arrival of these lungfishes to Australia, and then South America (see Agnolin 2010).

CHAPTER 3 - *CYCLOTOSAURUS NARASERLUKI*, SP. NOV., A NEW LATE TRIASSIC CYCLOTOSAURID (AMPHIBIA, TEMNOSPONDYLI) FROM THE FLEMING FJORD FORMATION OF THE JAMESON LAND BASIN (EAST GREENLAND)

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Marzola, M., O. Mateus, N. Shubin, and L. Clemmensen. 2017. *Cyclotosaurus naraserluki*, sp. nov., a new Late Triassic cyclotosaurid (Amphibia, Temnospondyli) from the Fleming Fjord Formation of the Jameson Land Basin (East Greenland). Journal of Vertebrate Paleontology 37(2), e1303501. DOI:10.1080/02724634.2017.1303501.

Abstract

Cyclotosaurus naraserluki, sp. nov., is a new Late Triassic capitosaurid amphibian from lacustrine deposits in the Fleming Fjord Formation of the Jameson Land Basin in Greenland. It is based on a fairly complete and well-preserved skull associated with two vertebral intercentra. Previously reported as *Cyclotosaurus* cf. *posthumus*, *C. naraserluki* is unique among cyclotosaurs for having the postorbitals embaying the supratemporals posteromedially. The anterior palatal vacuity presents an autapomorphic complete subdivision by a wide medial premaxillary-vomerine bony connection. The parasphenoid projects between the pterygoids and the exoccipitals, preventing a suture between the two, a primitive condition shared with Rhinesuchidae, *Eryosuchus*, and *Kupferzellia*. Within *Cyclotosaurus*, the Greenlandic skull has a distinctive combination of circular choanae (shared with *C. ebrachensis*, *C. posthumus*, and *C. robustus*) and a convex posteromedial margin of the tabulars (also present in *C. ebrachensis* and *C. intermedius*). A phylogenetic analysis indicates that *C. naraserluki* is the sister taxon of the middle Norian *C. mordax* from southern Germany, with which it shares a pair of premaxillary foramina. *Cyclotosaurus* is one of the most successful and diverse genera of Late Triassic temnospondyls, with at least eight species reported from middle Carnian to late Norian. *Cyclotosaurus naraserluki* is the largest amphibian ever reported from Greenland and one of the Late Triassic vertebrates with the highest northern paleolatitude currently known.

Introduction

Late Triassic lake deposits of Norian–?early Rhaetian age of the Fleming Fjord Formation are very well exposed along the margin of the Jameson Land Basin in East Greenland (Clemmensen 1980a, 1980b) (Fig. 3.1A-B). These lacustrine deposits have yielded a rich and diverse vertebrate fauna, including most of the main vertebrate groups known from the Late Triassic (Jenkins et al. 1994, 1997, 2001, 2008; Clemmensen et al. 1998, 2016; Gatesy et al. 1999; Milàn et al. 2012; Mateus et al. 2014; Sulej et al. 2014; Hansen et al. 2016; Marzola et al. 2016). The amphibian fauna reported from the Jameson Land Basin includes the plagiosaurid *Gerrothorax pulcherrimus* Fraas 1913 (Jenkins et al. 2008) and remains tentatively associated with the capitosaurid *Cyclotosaurus* Fraas 1889 (Jenkins et al. 1994; Sulej et al. 2014).

Cyclotosaurus belongs to a family of Late Triassic temnospondyl amphibians, the Cyclotosauridae, sensu Damiani (2001) and Schoch (2008), characterized by a dorsoventrally flat, elongated, parabolic skull, with eye sockets placed in the posterior half of the head, a long, laterally compressed tail, and relatively short limbs (Milner 1994; Rinehart and Lucas 2016). Moreover, at least four synapomorphies are known to identify cyclotosaurids: infraorbital canals curving over the lacrimals with a 'Z' shape, vomerine tusks positioned lateral to the palatal vacuity, a wide parabolic snout, and a vomerine palate as long as wide (Damiani 2001; Schoch 2008). Among the largest amphibians to have ever lived (total body length up to 3 m), cyclotosaurids were mostly piscivorous, semi-aquatic predators, colonizing freshwater niches, such as rivers and lakes, as well as coastal brackish to marine areas (Milner 1994; Fortuny et al. 2016; Witzmann et al. 2016).

In this study, we provide the first complete anatomical description and phylogenetic analysis of the capitosaurid skull reported in Jenkins et al. (1994) and associated vertebral intercentra. We support the original assignment of the Greenlandic specimen to the genus *Cyclotosaurus* based on the undoubted presence of seven of the eight synapomorphies given for this genus in Witzmann et al. (2016). *Cyclotosaurus naraserluki* is erected as a new species, based on a combination of autapomorphies and associated characters unique among known cyclotosaurids.

Materials and Methods

Cyclotosaurus naraserluki: holotype MGUH.VP 9522 (Figs. 3.2–3.5), a nearly complete skull on exhibit at the GeoCenter of Møns Klint, Denmark. Associated with the skull are two intercentra, MGUH.VP 9523 and MGUH.VP 9524 (Fig. 3.6). Locality: Macknight Bjerg Quarry, Jameson Land, Greenland (see Jenkins et al. 1994). Horizon and age: Late Triassic (late Norian) of the Fleming Fjord Formation (see Jenkins et al. 1994) (Fig. 3.1).

Other Taxa Used for Comparison from Personal Observation and the Literature

The following specimens were analyzed by personal observation of original material: *Cyclotosaurus intermedius* Sulej and Majer 2005: ZPAL Ab III 1173 (holotype); *C. mordax* Fraas 1913: SMNS 13014 (holotype), 50008, 50059, 50063, and 51102; *C. posthumus* Fraas 1913: SMNS 12988 (holotype); *C. robustus* von Meyer and Plieninger, 1844: SMNS 5775 (holotype), 4139, and 4935; *Eocyclotosaurus wellesi* Schoch 2000: UCMP 42841 (holotype), 41343, 41645, 41646, 55466, 123590, 123595, and 125364; *E. appetolatus* Rinehart et al. 2015: NMMNH P-64166 (holotype), 43126, 63328, 64360, 66832, and 67401; *Kupferzellia wildi* Schoch 1997: SMNS 54670 (holotype); and *Quasicyclotosaurus campi* Schoch 2000: UCMP 37754 (holotype), 41635, 132022, 172489, 172490, 172491, 172492, and

172493. Photos of *C. ebrachensis* Kuhn 1932, BSPG 1931 X 1 (holotype), were kindly provided by Dr. Oliver Rauhut.

From the literature, the following species were analyzed: *C. buechneri* (Witzmann et al. 2016:85, 87, figs. 2–3); *C. hemprichi* (Kuhn 1942:tables I–III); *Mastodonsaurus cappelensis* (Wepfer 1923); *M. giganteus* (Schoch 1999:150, fig. 54); *Paracyclotosaurus davidi* (Watson 1956:255, fig. 14); and *Procyclotosaurus stantonensis* (Paton 1974:256, fig. 1).

Phylogenetic Analysis

Cyclotosaurus naraserluki MGUH.VP 9522 was coded in the data set by Witzmann et al. (2016) for a total of 17 taxa and 69 characters (A1). Character 7 of Witzmann et al. (2016) was reformulated for the present analysis as character 7: Lateral line sulci: weakly impressed and discontinuous (0); continuous and well impressed (1); well impressed laterally and weakly impressed or discontinuousmedially (2). State 2 for character 7 was coded for *C. ebrachensis*, *C. hemprichi*, *C. mordax*, *C. naraserluki*, *C. posthumus*, and *C. robustus*. We used TNT 1.5-beta, available at www.lillo.org.ar/phylogeny/tnt (Goloboff and Catalano 2016). We performed an heuristic search, with 1000 replications using Wagner trees as starting trees, followed by tree-bisection-reconnection (TBR), retaining 10 trees per replication.

Geological Setting

The Fleming Fjord Formation is exposed in East Greenland at the Jameson Land Basin, between 70 and 73ºN (Clemmensen 1980a, 1980b; Clemmensen et al. 1998, 2016) (Fig. 1). During the Late Triassic, the Jameson Land Basin lay farther to the south, at around 40ºN (Kent and Clemmensen 1996; Kent and Tauxe 2005). The basin was located in a climatic transition zone of the Pangaea continent, between a relatively dry inland of the supercontinent and a more humid peripheral part (Clemmensen et al. 1998, 2016; Kent et al. 2014).

Three members of cyclically bedded lacustrine deposits from the Late Triassic Fleming Fjord Formation, with a thickness of 300–400 m are: the lowermost Edderfugledal Member, the middle Malmros Klint Member, and the uppermost Ørsted Dal Member (Clemmensen 1980a, 1980b; Clemmensen et al. 1998). The Ørsted Dal Member lies towards the eastern margin of the basin and is composed of a lowermost unit of red mudstones, the Carlsberg Fjord beds, and an uppermost unit of variegated mudstones and light gray dolomitic mudstones, the Tait Bjerg Beds (Jenkins et al. 1994; Clemmensen et al. 2016).

Temnospondyl amphibian remains have been reported from the easternmost part of the basin at the Macknight Bjerg Quarry (71º220N, 22º330W) in the lowermost part of the Carlsberg Fjord beds (Sulej et al. 2014; Clemmensen et al. 2016). The *Cyclotosaurus* specimen described here originates from this quarry (Jenkins et al. 1994).

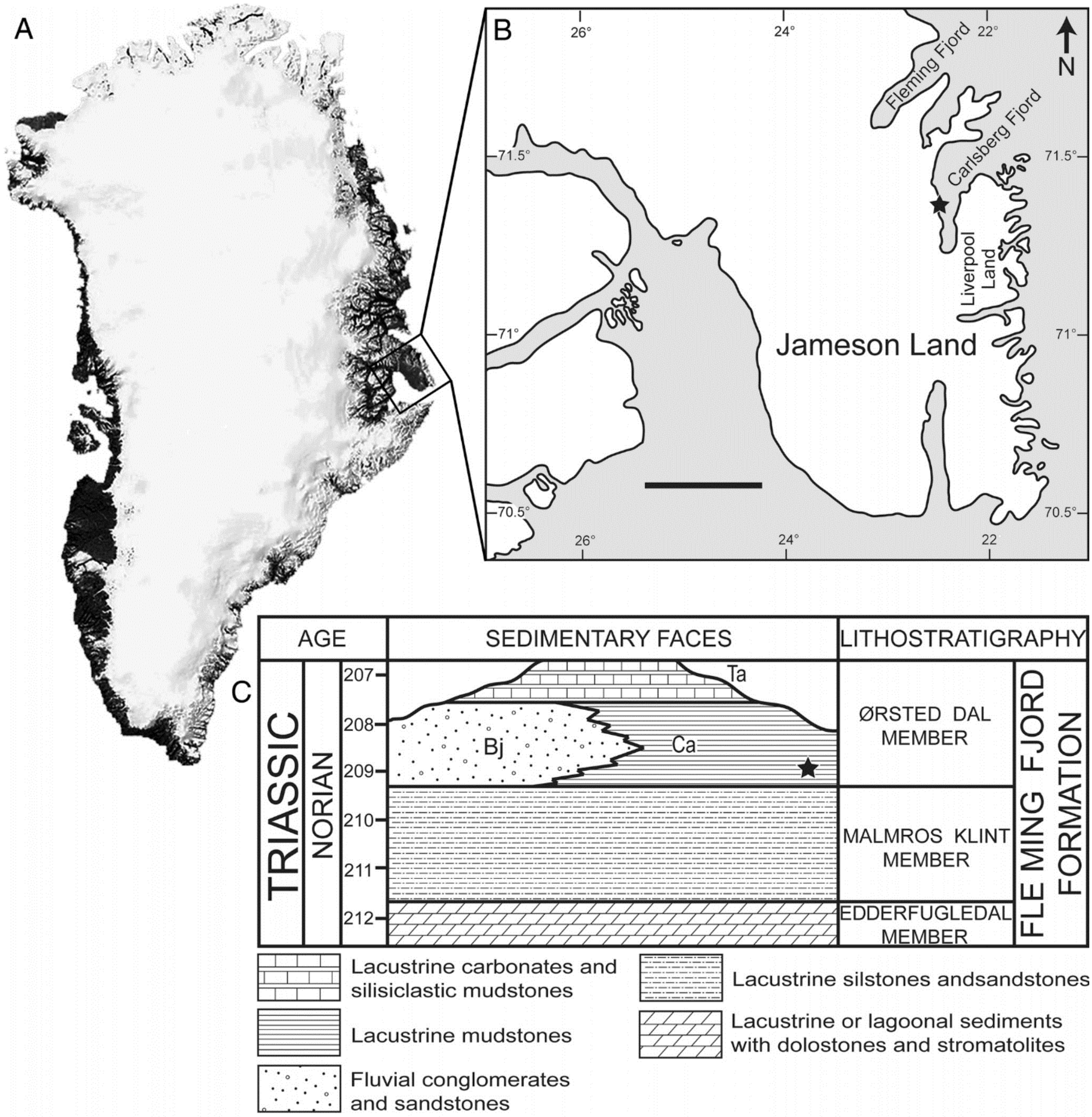

Figure 3.1 - A, geographical map of Greenland; B, close-up of Jameson Land and the Liverpool Land area; C, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al., 1998). Stars in B and C indicate the site where the holotype of *Cyclotosaurus naraserluki* was discovered. Abbreviations: **Bj**, Bjergkronerne beds; **Ca**, Carlsberg Fjord beds; **Ta**, Tait Bjerg Beds. Scale bar equals 40 km (B).

The Carlsberg Fjord beds are composed of siliciclastic sediments of mudflat and lake origin. The most common facies are red-brown to purple mudstones, light greenish-gray mud-peloid siltstones with wave ripples, intraformational conglomerate, and light grayish, fine- to medium-grained sandstones with current-formed crossstratification. Numerous *Grallator* and cf. *Brachychirotherium* tracks are seen on upper bedding planes of the wave-rippled siltstones, the former attributed to theropod dinosaurs and the latter to stemcrocodylians (Clemmensen et al. 2016; Klein et al. 2016).

According to Kent and Clemmensen (1996) and Clemmensen et al. (1998), the Macknight Bjerg Quarry at the base of the Carlsberg Fjord beds of the Ørsted Dal Member has an age of approximately 209 Ma. However, using the stratigraphy of Andrews et al. (2014), the site would be dated around 217 Ma. The age and duration of the Norian has seen considerable work (e.g., Kent and Olsen 1999; Lucas et al. 2012). According to the International Chronostratigraphic Chart (Cohen et al. 2013; latest version available at www.stratigraphy.org/ICSchart/Chrono stratChart2016-04.pdf), the Norian ranges from ~227 to ~208.5 Ma. However, U-Pb dating, biostratigraphy, magnetostratigraphy, and chemostratigraphy analyses place the Norian-Rhaetian boundary at about 205.70 ± 0.15 Ma (Wotzlaw et al. 2014; Bertinelli et al. 2016). Thus, an age estimate of the quarry site of 209 Ma (Clemmensen et al. 1998) would place it in the late Norian, whereas an age estimate of 217 Ma (Andrews et al. 2014) would give a mid-Norian age.

Systematic Paleontology

TEMNOSPONDYLI von Zittel, 1887–1890
STEREOSPONDYLI von Zittel, 1887–1890
CAPITOSAUROIDEA Säve-Söderbergh 1935
CYCLOTOSAURIDAE Shishkin 1964
CYCLOTOSAURUS Fraas 1889
CYCLOTOSAURUS NARASERLUKI, sp. nov.
(Figs. 3.2–3.6)

Cyclotosaurus cf. *posthumus* Fraas 1913: Jenkins et al. 1994:7–8, figs. 4–5 (original report); Schoch 2008:202.

Cyclotosaurus, sp. nov.: Schoch and Milner 2000:156.

Cyclotosaurus posthumus Fraas 1913: Damiani 2001:404.

Holotype—MGUH.VP 9522 (previously V-2012-146a, as on the label on the specimen), a mostly complete skull, 56.8 cm in length along the midline from the tip of the snout to the posterior end of postparietals and with a maximum width of 42.4 cm (Figs. 3.2–3.5; Supplementary Data 3.1, 3.2).

Associated Material—MGUH.VP 9523 and MGUH.VP 9524 (previously V-2012-268 and V-2012-269, respectively, as on the labels on the specimens), two vertebral intercentra (Fig. 3.6).

Type Locality—The type specimens were collected during the 1989 expedition to Macknight Bjerg Quarry (71°22.300N, 22°33.140W), at Jameson Land, East Greenland (Fig. 3.1).

Type Horizon—Late Triassic Carlsberg Fjord beds (Ørsted Dal Member) of the Fleming Fjord Formation (Fig. 3.1).

Etymology—The specific name is after 'naraserluk,' Greenlandic for 'amphibian, salamander'.

Diagnosis—*Cyclotosaurus naserluki* has the following autapomorphies among other *Cyclotosaurus* species: (1) the postorbitals notching posteromedially in the supratemporals; (2) the

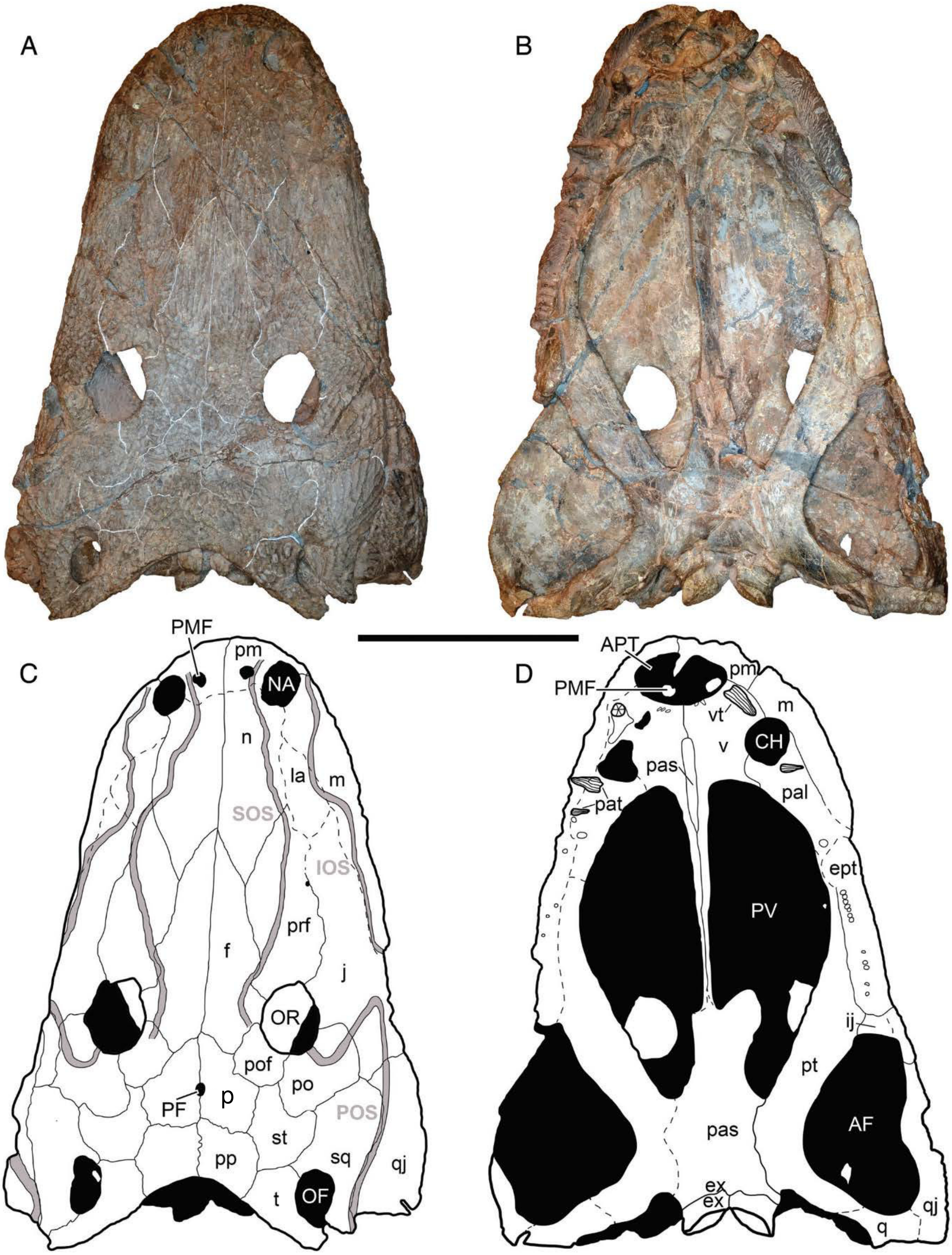

Figure 3.2 - The holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522. A, C, photograph and interpretative drawing of dorsal view; B, D, photograph and interpretative drawing of ventral view. Abbreviations: **AF**, adductor fossa; **APV**, anterior palatal vacuity; **CH**, choana; **ex**, exoccipital; **ept**, ectopterygoid; **f**, frontal; **ij**, insula jugalis; **IOS**, infraorbital sulcus; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **NA**, naris; **OF**, otic fenestra; **OR**, orbit; **p**, parietal; **pal**, palatine; **pas**, parasphenoid; **pat**, palatine tusk; **PF**, parietal foramen; **PMF**, premaxillary foramen; **pm**, premaxilla; **pof**, postfrontal; **POS**, postorbital sulcus; **po**, postorbital; **pp**, postparietal; **PQF**, paraquadrate foramen; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **PV**, palatal vacuity; **q**, quadrate; **qj**, quadratojugal; **s**, squamosal; **st**, supratemporal; **SOS**, supraorbital sulcus; **t**, tabular; **to**, tooth; **v**, vomer; **vt**, vomerine tusk. Scale bar equals 20 cm.

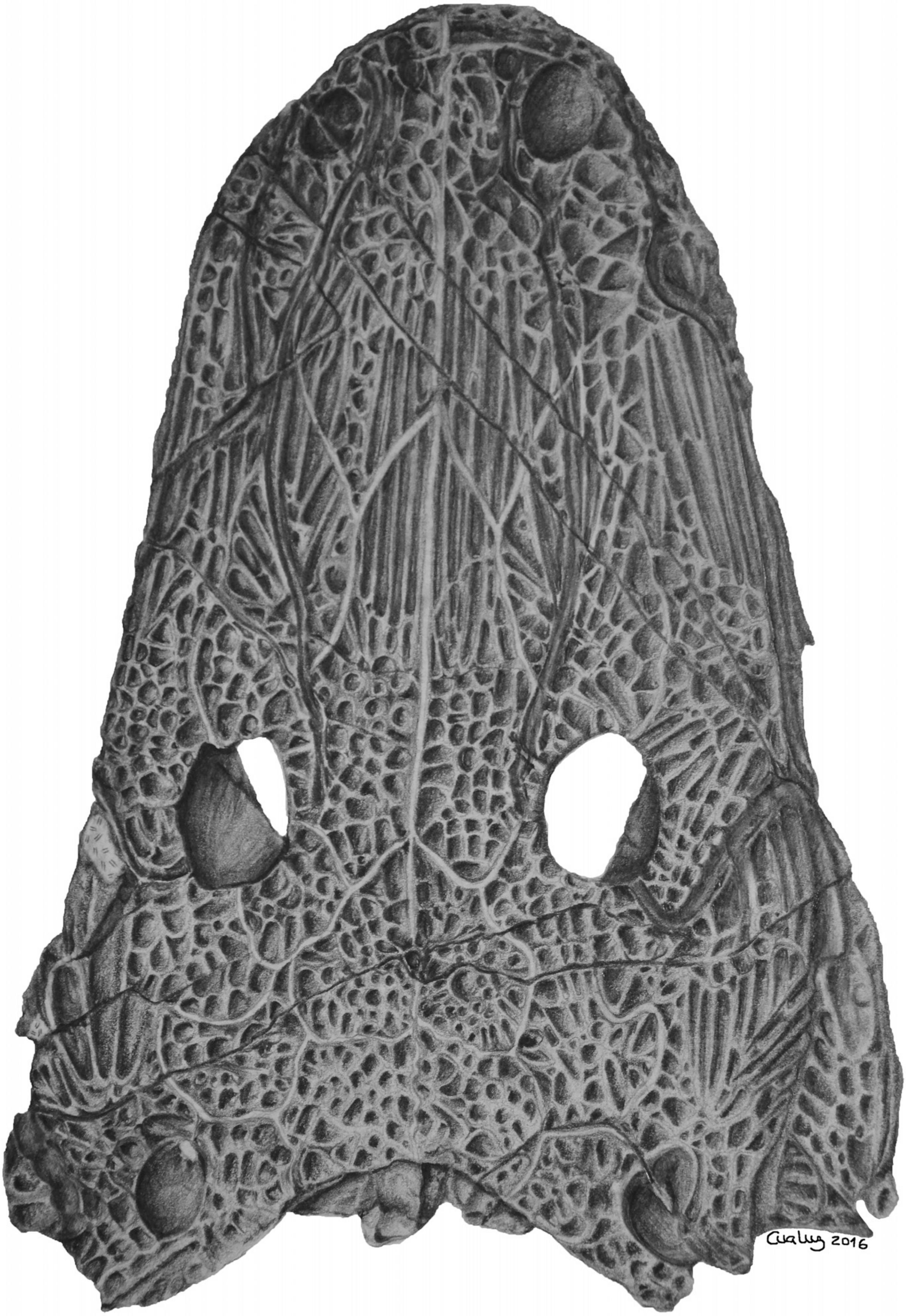

Figure 3.3 - Artwork of the dorsal view of the holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522, by Ana Luz (Museu da Lourinhã).

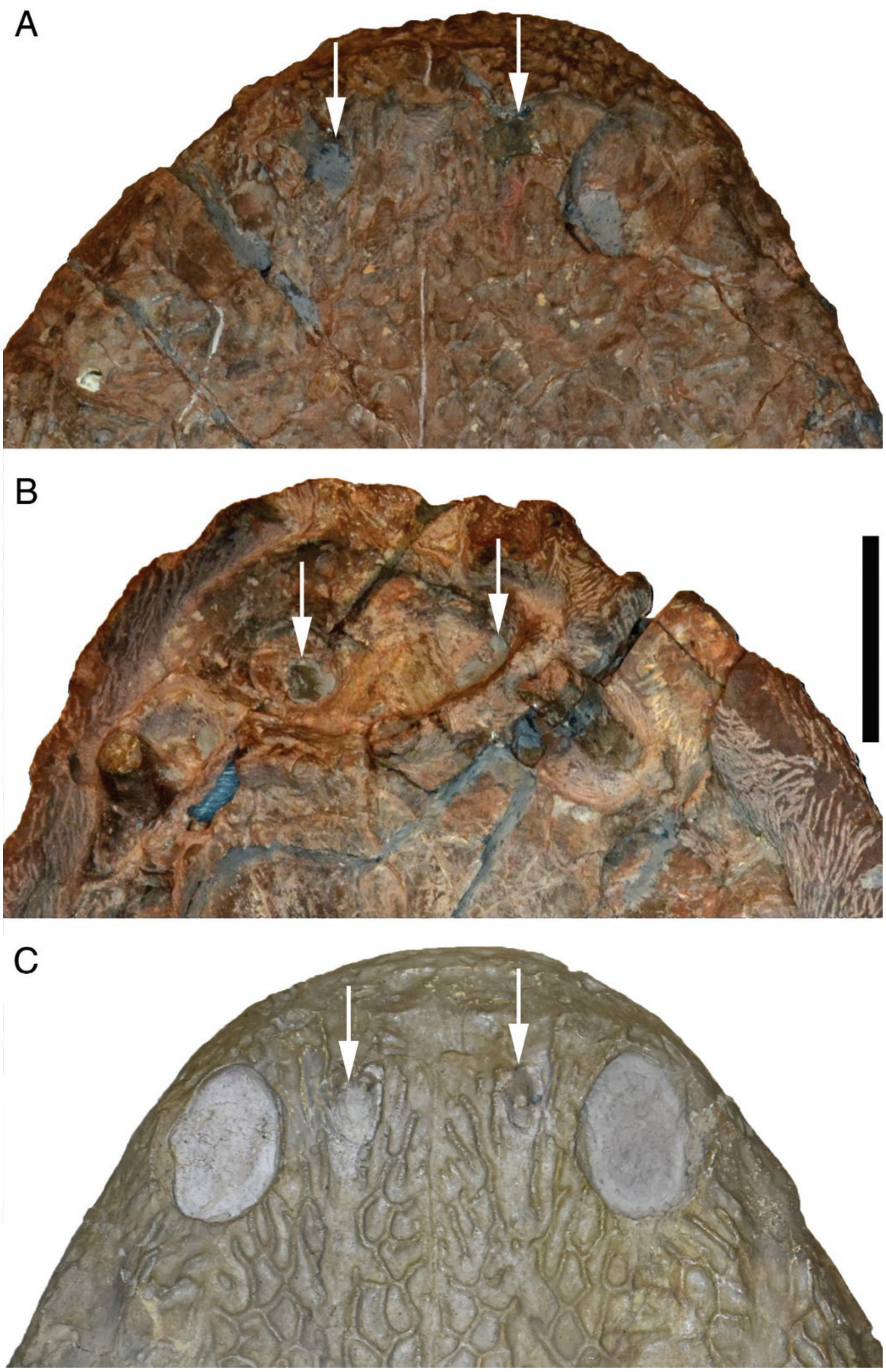

Figure 3.4 - Close-up views of the premaxillary foramina (highlighted by white arrows) in cyclotosaurids. A, B, dorsal and ventral views of the holotype of *Cyclotosaurus naraserluki*, MGUH.VP 9522; C, holotype of *Cyclotosaurus mordax*, SMNS 13014. Scale bar equals 5 cm.

parasphenoid projecting between the pterygoids and the exoccipitals, thereby preventing a pterygoid-exoccipital suture; and (3) the anterior palatal vacuity is subdivided by a wide medial connection of the premaxillae and the vomers. Moreover, *C. naraserluki* has the following unique combination of characters among *Cyclotosaurus*: (1) a pair of premaxillary foramina for accommodating mandibular tusks (shared with *C. mordax*, see Fig. 3.4); (2) a posteromedial convex margin of the tabulars (shared with *C. ebrachensis* and *C. intermedius*, doubtfully with *C. mordax*); and (3) a circular choanal outline (shared with *C. ebrachensis*, *C. posthumus*, and *C. robustus*).

Description

General Aspect and Dermal Bone Ornaments—The entire skull MGUH.VP 9522 (Figs. 3.2–3.5; Supplementary Data 3.1, 3.2) is very well preserved. The skull outline is parabolic, with a widely parabolic snout and convex lateral margin of the postotic region. The only appreciable missing part is the posterior contact of the right tabular and squamosal, which leaves the right otic fenestra open posteriorly. Some sutures and contacts between bones, especially from the posterior part of the skull, are not visible due to lack of preparation and sediment still present on the specimen. A slight deformation seems to affect the entire left half of the skull. The bone sutures are more evident in the posterior half of the skull, fading almost to complete fusion anteriorly. Skull length is 56.8 cm, as measured along the midline suture, from the tip of the snout to the posterior end of the postparietals. The maximum width is 42.4 cm, measured at the maximum distance between the lateral margins of the quadratojugals.

Cyclotosaurus naraserluki presents the typical dorsal ornamentation of temnospondyl skulls. Subcircular to subpentagonal pits and a reticular pattern of ridges cover most of the skull roof, especially evident on the tip of the snout, as well as all over the parietals and the postparietals. Ridges and anteroposteriorly elongated ornamentation are evident in the posteromedial region of the snout, covering most of the frontals and part of the nasals and prefrontals. This elongated ornamentation is associated with intensive growth of the skull (Bystrow 1935). The same kind of ridgeelongated sculpture is evident in the postorbital regions, covering most of the squamosals and part of the postorbitals, the jugals, and the quadratojugals.

Lateral Line Sulci

The lateral line sulci in *C. naraserluki* are present as pairs of supraorbital, infraorbital, and postorbital sulci. They are more evident laterally, especially in the posterior part of the skull, and weakly impressed medially, especially across the snout.

Supraorbital Sulci—The supraorbital sulci originate on the anterior part of the snout, medially to the nares. They meander anteroposteriorly from the nasals to the prefrontals, reaching theposterior part of the frontals, and weakly ending on the postfrontals, at around the midline of the orbits. Regardless of the weak preservation of both lacrimals, the left supraorbital sulcus seems to run along the suture between the prefrontal and the lacrimal, like in other cyclotosaurids and temnospondyls (see Schoch 2008; Rinehart et al. 2015; Rinehart and Lucas 2016; Witzmann et al. 2016).

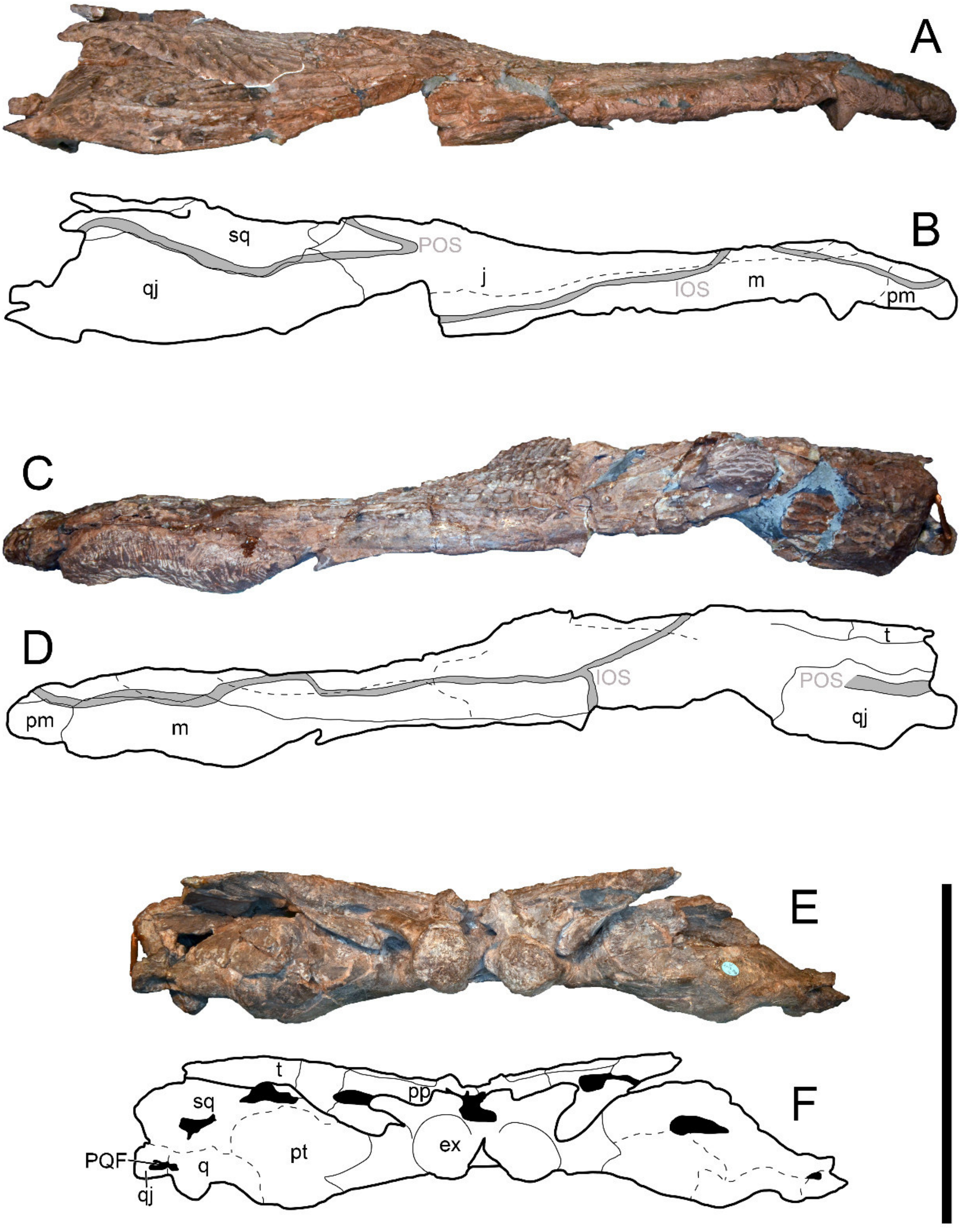

Figure 3.5 - The holotype specimen of *Cyclotosaurus naraserluki*, MGUH.VP 9522. A, B, photograph and interpretative drawing of right lateral view; C, D, photograph and interpretative drawing of left lateral view; E, F, photograph and interpretative drawing of occipital view. Abbreviations: **ex**, exoccipital; **IOS**, infraorbital sulcus; **j**, jugal; **m**, maxilla; **pm**, premaxilla; **POS**, postorbital sulcus; **pp**, postparietal; **PQF**, paraquadrate foramen; **pt**, pterygoid; **sq**, squamosal; **q**, quadrate; **qj**, quadratojugal; **t**, tabular. Scale bar equals 20 cm.

Infraorbital Sulci—The infraorbital sulci originate lateral to the nares, first meandering anteroposteriorly on the maxillae, then curving with an acute flexure onto the lacrimals, ending atop or parallel to the jugal-maxilla sutures.

Postorbital Sulci—The postorbital sulci originate from the postorbital rim of the orbits. They run with a 'S'-shaped curvature onto the jugals and the quadratojugals at first, then along the squamosal-quadratojugal sutures, ending at the posterior margin of the skull.

Skull Roof

Teeth—Complete and incomplete labyrinthodont teeth are visible ventrally, protruding both from the vomers and the palatines as tusks, anteriorly to the palatal vacuities. These tusks have a conical shape and a circular cross-section. The vomers also bear six small teeth medially located posterior to the anterior palatal vacuity. Tooth alveoli are seen along the maxillae, the palatines, and the ectopterygoids, organized in rows.

Premaxillae—The premaxillae form the anterior-most rim of the snout and contact medially. In dorsal view, they contact the nasals posteriorly, the maxillae laterally, and form part of the nares rims. In ventral view, the premaxillae contact the maxillae laterally, the vomers posteriorly, and form the anterior half of the rim of the anterior palatal vacuity. The premaxillae bear the two premaxillary foramina for the accommodation of the mandibular tusks.

Maxillae—The maxillae form the major part of the lateral skull margin, extending from the anterior part of the nares to the midlength of the skull, up to the anterior margin of the orbits. Dorsally, they contribute to the lateral rim of the nares. The maxillae are bordered anteriorly by the premaxillae and medially by the nasals, the lacrimals, and the jugals. Ventrally, they contact the premaxillae anteromedially, the vomers and the palatines medially. They contribute to the anterolateral rim of the choanae.

Nasals—The nasals form most of the anterior part of the snout. Subrectangular in shape, they pair medially and contact the premaxillae anteriorly. Posteriorly, they taper to a triple point with the frontals posteromedially and the prefrontals posterolaterally. Laterally, the nasals contact first the maxillae behind the nares, then the lacrimals. Anterolaterally, they contribute to the narial rims.

Lacrimals—The lacrimal sutures are very faint. The right lacrimal seems to have a drop shape, with a wider parabolic posterior suture, where it contacts the prefrontal medially and the jugal laterally, and a more tapered anterior suture, where it is bordered by the nasal medially and the maxilla laterally. Ventrally, there are no visible sutures between the lacrimals and the bordering bones.

Jugals—The jugals form most of the cheek regions. Their total contribution to the length of the snout cannot be clearly delineated due to the weak preservation of the anterior sutures. Anteriorly, they taper at the contact with the lacrimal-maxilla suture, although this suture is faintly visible only on the right jugal. Medially, the jugal-maxilla suture runs anteroposteriorly. Laterally, the jugals are bordered by the prefrontals anterior to the orbits and by the postorbitals posterior to the orbits. The postorbital-jugal suture runs with a 'Z'-shaped outline until reaching a triple point, where the jugals are bordered by the squamosals medially and the quadratojugals laterally. The jugals contribute to form a small part of the orbital rim.

Prefrontals—The prefrontals are two elongated bones that narrow anteriorly to a three-point suture with the nasals anteromedially and the lacrimals anterolaterally. Almost as long as the nasals and the frontals, they contact the former medioanteriorly and the latter medioposteriorly. Laterally, the jugals contact anteriorly the lacrimals and laterally the jugals; posteriorly, they form the anteriormost rim of the orbits.

Frontals—The frontals contact along the midline from the medial part of the snout until reaching the posterior level of the orbits. With a subtriangular anterior outline, they are bounded by the nasals anteriorly, forming a straight suture. The frontalprefrontal sutures run laterally, first with a straight course, then with a sigmoid curvature. Posteriorly, the frontals present a 'W'- shaped suture, defined by the parietals posteromedially and by the postfrontals posterolaterally. The frontals contribute to a narrow portion of the orbital rim, projecting between the prefrontals and the postorbitals.

Postfrontals—The postfrontals have a subcircular shape and contribute to the posteromedial rim of the orbits. Anteriorly, they contact the frontals and are bordered by the parietals posteromedially, the supratemporals posteriorly, and the postorbitals laterally.

Postorbitals—The postorbitals have a subtrapezoidal shape and contribute to the posterolateral rim of the orbits. Medially, they contact the postfrontals and embay into the supratemporals posteromedially, projecting more laterally than the orbits. The postorbitals contact the jugals and the squamosals laterally.

Quadratojugals—The quadratojugals form the posterior-most side of the cheeks and the lateral-most part of the skull. In dorsal view, they have a subrectangular shape and contact the jugals anteriorly and the squamosals medially, along a sigmoidal suture. In ventral view, they contact the insulae jugalis anteriorly and the quadrates medially. They form a big part of the lateral and posterior rims of the adductor fossae. In occipital view, the quadratojugals contact the quadrates medially and the squamosals dorsally. In posterior view, the general aspect of the *C. naraserluki* skull appears to be rounded, with a slight deformation to the right side, probably due to taphonomy.

Parietals—The parietals contact medially, and they form a heart-shaped outline, with the tip facing anteriorly. They enclose the parietal foramen posteriorly to the midlength of their medial suture. They contact the frontals anteriorly, the postfrontals and the supratemporals laterally, and the postparietals posteriorly.

Supratemporals—The supratemporals present an arcuate shape, with the concavity projecting posteromedially. Anteriorly, the supratemporals embay the postorbitals and slightly contact with the postfrontals. The supratemporals contact the parietals medioanteriorly, by a straight suture, and the postparietals medioposteriorly, by an anterolaterally concave suture. The posteromedial supratemporal suture is a gentle curve contacting the squamosals and the tabulars.

Squamosals—The squamosals form a small part of the posterior rim of the skull, projecting between the quadratojugals and the tabulars. They contact the postorbitals and the jugals anteriorly, the supratemporals and the tabulars medially, and the quadratojugals laterally. The tabular-squamosal suture is fully visible in the left side of the skull, where it runs posterolaterally. The squamosals contribute to form about half of the otic fenestra rims.

Postparietals—The postparietals contact along the posteriormost part of the midline and form the posterior concavity of the dorsal rim of the skull. Different from the rest of the midline, the contact between the two postparietals is not straight but follows a zig-zag course. The postparietal-parietal sutures extend mediolaterally, whereas the lateral contact with the supratemporals and the tabulars curves with a lateral concavity.

Tabulars—The polygonal shape of the tabulars broadens anteriorly and ends along the posterior, slightly convex margin of the skull. They contact the supratemporals anteriorly, the postparietals medially, and the squamosals laterally along a suture that embays the otic fenestra. The suture between the tabular and the squamosal is only appreciable posteriorly to the left otic fenestra. In dorsal view, the tabular horns project laterally. Also, they are the posterior-most projecting bones of the skull.

Endocranium

Quadrates—Ventrally, the quadrates present a polygonal shape that contacts the pterygoids medially and the quadratojugals laterally. The sutures of the quadrates are not clearly exposed or preserved. Anteriorly, the quadrates form part of the posterior rim of the adductor fossae, whereas posteriorly they contribute to the posterior margin of the skull.

Exoccipitals—The exoccipitals contact ventromedially and suture with the parasphenoid anteriorly. They project posteriorly to form the articulation with the atlas and diverge dorsally to enclose the ventral part of the foramen magnum. The posterior projection of the exoccipitals falls at the same level as the posterior-most projection of the quadrates. The posterior contact surfaces of the exoccipitals with the atlas are suboval in shape and flat.

Palate

Vomers—Anteriorly, the vomers form the posterior rim of the anterior palatal vacuity. Immediately behind this opening, six teeth are borne by the vomers, two by the left vomer and four by the right one, all set in a transverse row. The vomers also bear the first couple of palatal tusks. Anterolaterally, the vomers contact the premaxillae and the maxillae. Laterally, the vomers only contact the palatines and contribute to part of the choanae and to most of the medial rim of the palatal vacuities. The left vomer has a small posterolateral projection into the palatine. In ventral view, the vomers contact anteriorly, forming the posterior rim of the anterior palatal vacuity and the posterior part of the premaxillary-vomerine subdivision. Along the midline, the vomers contact one another except for the enclosure of the cultriform process of the parasphenoid. At their contact along the palatal vacuities, the vomers form a 'V'-shaped ridge that projects ventrally. The posterior contact between the vomers and the parasphenoid is weak.

Palatines—The palatines have a subrectangular shape and bear the second pair of palatal tusks. The right palatine also bears the third palatal tusk, which is not preserved on the left counterpart. Anteriorly, the palatines form the posterior rim of the choanae and contact the maxillae. The palatine-maxilla sutures run posterolaterally from the choanae to the ectopterygoid. Medially, the palatines contribute to the rim of the palatal vacuities. The posterior contact between the palatines and both the pterygoids and the ectopterygoids are indistinct.

Pterygoids—The pterygoids have a sinusoidal shape, extending between the palatal vacuities and the adductor fenestrae and forming part of their respective rims. Anteriorly, the pterygoids contact the palatines. Medially, the sutures that separate the pterygoids from the ectopterygoids and the insulae jugalis are poorly preserved to indistinguishable, except for the left pterygoid– insula jugalis suture. Posteriorly to the adductor fossae, the pterygoids contact the quadrates and form part of the posterior margin of the skull. The medial contact between the pterygoids and the parasphenoid is weakly noticeable. The right pterygoid bears a weak ornamentation anterior to the adductor fossa rim.

Parasphenoid—The parasphenoid is an unpaired, midline bone. Anteriorly, the cultriform process of the parasphenoid extends beyond the anterior margin of the palatal vacuities, enclosed by the vomers. The cultriform process projects ventrally, forming a keel-like structure that narrows posteriorly. The parasphenoid-exoccipital suture has a flat and long 'M' shape. The crista muscularis of the parasphenoid is an unpaired structure running transversely. Laterally, the parasphenoid contacts the pterygoids, although the sutures are barely visible. Nonetheless, it looks like the parasphenoid-pterygoid sutures are as long as the width of the parasphenoid basal plate. The left parasphenoid-pterygoid suture is the best preserved and ends at the posterior embayment of the skull margin, avoiding the contact between the pterygoids and the exoccipitals, a primitive condition shared with Rhinesuchidae, Eryosuchus Ochev 1966, and Kupferzellia. The parasphenoid contributes to the posteromedial rim of the palatal vacuities and presents a left anterior protuberance, probably due to taphonomic deformation.

Ectopterygoids—The ectopterygoids are not easily observed in the palate of *C. naraserluki* because they are not completely prepared. Nonetheless, the left ectopterygoid preserves a somewhat distinct medial suture with the pterygoid and a posterior suture with the insula jugalis. The right ectopterygoid bears at least three distinct alveoli organized in a row, whereas the left ectopterygoid bears at least 12 distinct alveoli organized in an anteroposteriorly oriented row.

Insulae Jugalis—The insulae jugalis are weakly preserved. The right insula jugalis is nearly indistinguishable, whereas the left insula jugalis presents a trapezoid shape. It bounds the ectopterygoid anteriorly, the pterygoid medially, the quadratojugal laterally, and posteriorly it forms the anterior-most margin of the adductor fossa.

Skull Openings

Nares—The nares are two oval dorsal openings in the anterior part of the snout, with a maximum width of 3.5 cm. They are bounded by the premaxillae, the maxillae, and the nasals.

Premaxillary Foramina—*C. naraserluki* skull bears two premaxillary foramina for the reception of the mandibular tusks (Fig. 4). These two circular openings are filled with grayish sediment and noticeable on the dorsal surface of the skull, where they are enclosed completely by the premaxillae. Dorsally, the premaxillary foramina are evident in the anterior palatal vacuity.

Orbits—The orbits are the major openings of the dorsal side of the skull, with a maximum width of 5.5 cm and a subcircular outline. They are rimmed by the prefrontals, the frontals, the postfrontals, the jugals, and the postorbitals. The dorsal margin of the orbits is level with the rest of the skull roof.

Parietal Foramen—The parietal foramen is the smallest of the skull openings and the only unpaired one. Its maximum width is 1.1 cm, and it is completely enclosed by the parietals.

Otic Fenestrae—The otic fenestrae characterize the posterior skull roof and are bounded by the squamosals and the tabulars. The left otic fenestra is an oval cavity, elongated anteroposteriorly, with a maximum width of 4.5 cm. The right otic fenestra is posteriorly open due to the missing portion of the posterior contact between the squamosal and the tabular.

Anterior Palatal Vacuity—The anterior palatal vacuity is an ‘U’-shaped depression with a maximum length of 4.9 cm and width of 11.3 cm. It is enclosed by the premaxillae and the vomers. The anterior palatal vacuity presents the premaxillary foramina, two subcircular openings filled with sediment.

Choanae—The choanae are two circular cavities in the anterior part of the palate with a maximum width of 4.4 cm. Only the left choana preserves its original shape, whereas the right choana is deformed.

Palatal Vacuities—The palatal vacuities are the biggest openings of the palate, with a ‘D’-shaped outline, a maximum length of 28.9 cm, and a maximum width of 10.9 cm. The marginal rims are almost straight, whereas laterally they present a parabolic curvature with the posterior curvature more acute than the anterior one. The palatal vacuities are enclosed by the vomers, the palatines, the pterygoids, and the parasphenoid.

Adductor Fossae—The adductor fossae characterize the posterior- most region of the palate. The left adductor fossa is the best preserved and presents an arch shape with a gentle lateral convexity and a more acute medial concavity. The maximum length measured parallel to the midline is 16.9 cm, and the maximum width is 10.4 cm.

Postcranial Skeleton

Vertebrae—Two amphicoelic intercentra represent the only preserved postcranial elements of *C. naraserluki* (Fig. 3.6). They display a convex ventral surface, with a ventral thickness of 21 mm in MGUH.VP 9523 and 22 mm in MGUH.VP 9524. Dorsally, they are characterized by a central dorsoventral depression that also compresses the two intercentra anteroposteriorly down to 11 mm in thickness for MGUH.VP 9523 and down to 13 mm for MGUH.VP 9524. In MGUH.VP 9523 the maximum width is 42 mm and the maximum height is 25 mm, whereas MGUH.VP 9524 has a maximum width of 48 mm and height of 37 mm. Among other capitosauroids, these kinds of intercentra have so far only been reported from *Mastodonsaurus* Jaeger, 1828, and *Cyclotosaurus hemprichi* (Kuhn 1942; Schoch 1999). Intercentra of similar size and morphology have been further described by Milner et al. (1996) from the Norian of Luxemburg and the ?Carnian–Norian of Algarve in Portugal (Witzmann and Gassner 2008), the latter associated to stereospondyls, such as *Mastodonsaurus* and *Cyclotosaurus*. However, the material from Portugal is questionable: new well-documented discoveries from the Algarve (Steyer et al. 2011; Brusatte et al. 2015) show the presence of *Metoposaurus algarvensis*

Figure 3.6 - MGUH.VP 9523 (A–F) and MGUH.VP 9524 (G–L), vertebral intercentra associated with *Cyclotosaurus naraserluki*. A, G, anterior view; B, H, posterior view; C, I, right lateral view; D, J, left lateral view; E, K, dorsal view; F, L, ventral view. The visible labels on specimens refer to a former labeling system. Scale bars equal 2 cm.

Brusatte et al. 2015, which may suggest a need to reassess the identification of the previous fragmentary material (Witzmann and Gassner 2008).

Phylogenetic Results

The phylogenetic analysis yielded one most parsimonious tree (Figs. 3.7, 3.8), with a tree length (TL) of 109 steps and consistency index (CI) of 0.624, retention index (RI) of 0.680, and rescaled consistency index (RCI) of 0.424. Because of the recoding of character 7 and the addition of *C. naraserluki*, our phylogeny of *Cyclotosaurus* is slightly different from the one presented in Witzmann et al. (2016). *Cyclotosaurus* loses one synapomorphy (char. 48-1, quadrate ramus of the pterygoid laterally aligned and abbreviated) and the synapomorphy based on character 7 passes from state 0, 'lateral line sulci weakly impressed, discontinuous,' to state 2, 'lateral line sulci well impressed laterally but weakly impressed or discontinuous medially.' In general, most of the groups within Capitosauroidea (sensu Schoch 2008) are poorly supported, with the exception of the genus *Mastodonsaurus* and the Heylerosauridae (sensu Schoch 2008), which includes *Eocyclotosaurus* Ortlam 1970, and *Quasicyclotosaurus*. Moreover, despite presenting seven synapomorphies, the genus *Cyclotosaurus* is not well supported and may easily collapse due to the numerous reversals. New data and characters may help to overturn and increase the precision of the relations between these species.

Cyclotosaurus robustus remains the most basal *Cyclotosaurus* taxon, a position supported by a cultriform process that forms a deltoid base (char. 52-1). The remaining *Cyclotosaurus* taxa possess a preorbital projection of the jugals shorter than half of the snout length (reversal for char. 13-0). *Cyclotosaurus buechneri* presents lateral line sulci weakly impressed and discontinuous (reversal for char. 7-0). All post-*C. buechneri* cyclotosaurs have an interorbital width to width of the orbits ratio equal to or greater than 1.8 (char. 68-1). *Cyclotosaurus hemprichi* and *C. posthumus* are sister taxa, a relationship supported by a tapered preorbital region (char. 1-1) and an elongated parabolic snout (reversal for char. 66-0). A straight-to-convex posteromedial margin of the tabulars (char.69-1) is synapomorphic for the remaining four species of *Cyclotosaurus*, which branch into two clades. The clade formed by *C. naraserluki* and *C. mordax* is supported by a snout bearing a pair of premaxillary foramina to accommodate mandibular tusks (char. 57-1). The second clade includes *C. intermedius* and *C. ebrachensis*. It is supported by the presence of palatal denticle fields borne on the parasphenoid and/or the pterygoid (char. 32-0) and straight postorbital lateral margins of the skull (char. 67-1). *Cyclotosaurus intermedius* is supported by having the quadrates projecting posteriorly to the distal ends of the tabular horns (char. 2-0) and a weakly and discontinuous impression of the lateral sulci (reversal for char. 7-0). *Cyclotosaurus ebrachensis* is supported by supraorbital sulci passing over the nasals (reversal for char. 10-0) and by an unpaired anterior palatal vacuity (reversal for char. 20-0).

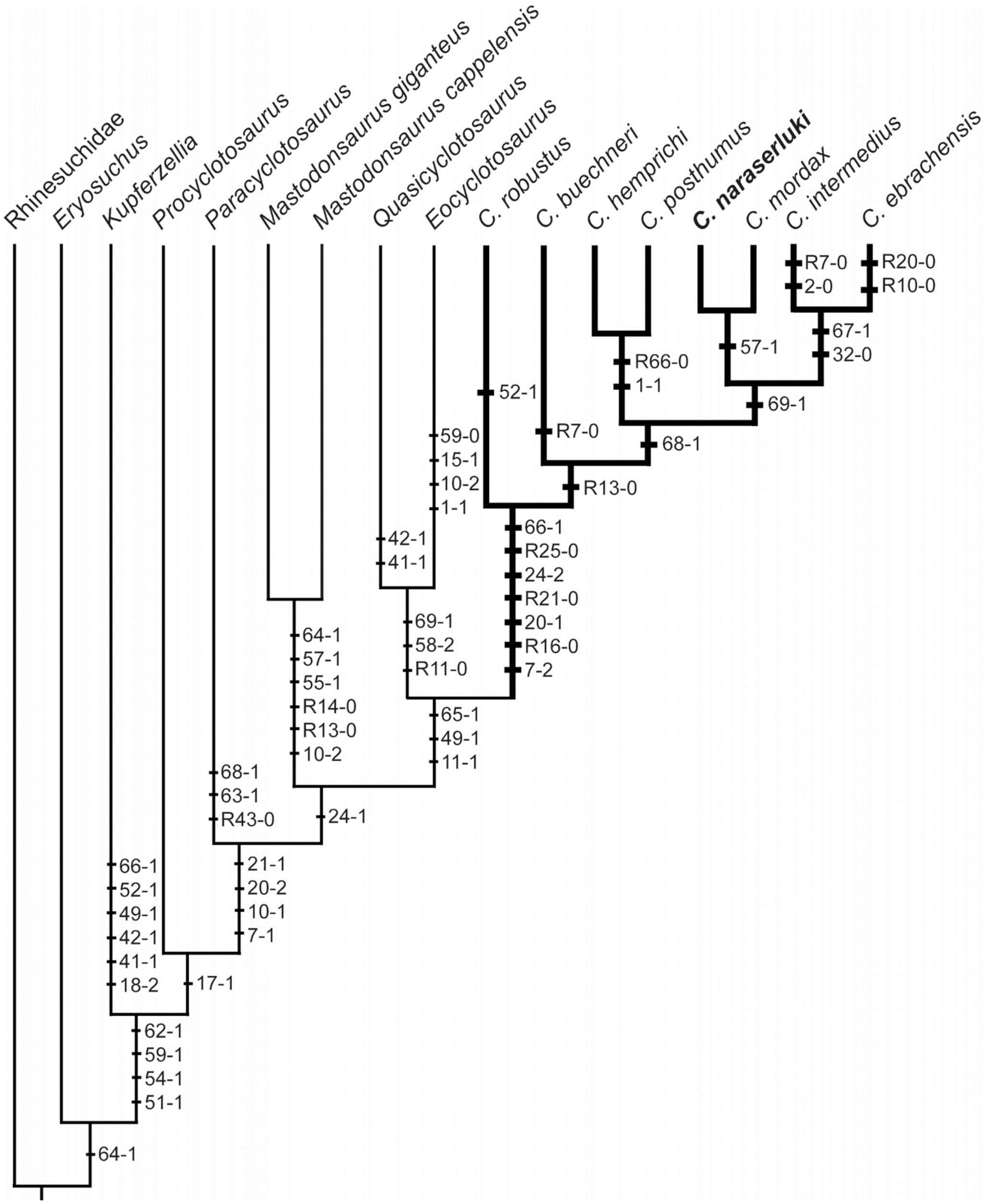

Figure 3.7 - Most parsimonious tree of the Capitosauroidea (sensu Schoch, 2008) produced by a TNT 1.5 analysis (tree length D 109 steps, consistency index D 0.624, retention index D 0.680, rescaled consistency index D 0.424). Synapomorphies are shown along the tree and numbers refer to the characters listed in the phylogeny in Witzmann et al. (2016). Thicker branches represent the genus *Cyclotosaurus* in the analysis. Abbreviations: **C.**, *Cyclotosaurus*; **R**, reversal.

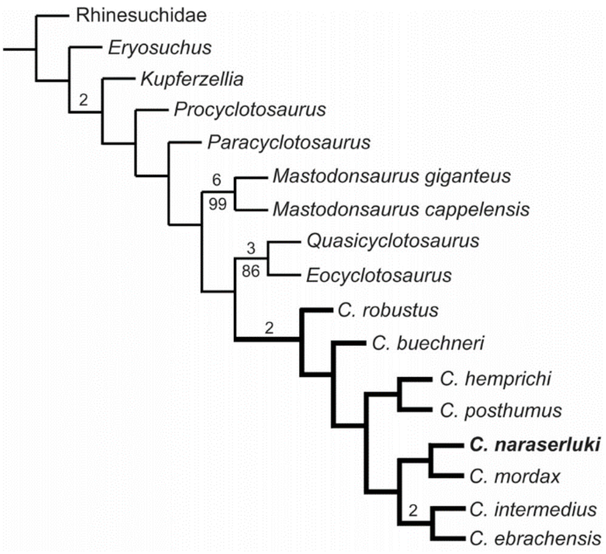

Figure 3.8 - Most parsimonious tree presented in Figure 7 showing Bremer support values (number over the branches) >1 and bootstrap values (numbers under the branches) after 1000 replicates.

Discussion

Paleoecology and Paleogeography

The remains here described belong to a new species of *Cyclotosaurus*, namely, *C. naraserluki*, sp. nov., the largest amphibian reported from Greenland heretofore (Jenkins et al. 1994, 2008). *Cyclotosaurus naraserluki* shared its living habitat with other semiaquatic amphibians and reptilian predators, such as *Gerrothorax pulcherrimus* (Jenkins et al. 2008) and phytosaurs (Mateus et al. 2014; Clemmensen et al. 2016; Marzola et al. 2016). The co-occurrence of *Cyclotosaurus* with other predators in the same area is consistent among all the known Late Triassic faunal associations from Europe where *Cyclotosaurus* has been reported (i.e., Sulej and Majer 2005; Witzmann and Gassner 2008). In the Greenland scenario, this may be explainable by different predatory habits, strategies, and physiological capacities of different taxa over the coasts of a huge seasonal lake in the Jameson Land Basin: large phytosaurs were actively preying on large terrestrial vertebrates and fish, like modern crocodiles; *Cyclotosaurus* and *Gerrothorax* were probably sharing ecological niches, but with the former being larger in size and preying mostly on fish, and the latter feeding on small fish, larvae, and invertebrates.

The Late Triassic Greenland fauna shows more affinities to European occurrences (dominated by genera such as *Cyclotosaurus*, *Gerrothorax* Nilsson 1934, *Mastodonsaurus*, *Metoposaurus* Lydekker 1890, and *Procyclotosaurus* Watson 1958) than to North American ones. In the Late Triassic, there is a clear distinction between the European-Greenlandic and the North American faunas, with the unique presence in the latter of *Apachesaurus* Hunt 1993, *Eocyclotosaurus*, *Koskinonodon* Branson and Mehl 1929, *Paracyclotosaurus*, and *Quasicyclotosaurus* (Watson 1958; Jenkins et al. 1994, 2008; Schoch

1999, 2000; Sulej 2002; Brusatte et al. 2015; Kear et al. 2016b; Rinehart et al. 2015; Rinehart and Lucas 2016).

Greenland is, and always has been, part of the North American continent, and despite the early opening of the North Atlantic, the Triassic fauna and flora show more affinities to the one in central Europe. This may be explained by several factors: (1) the equivalent paleolatitude of Greenland and central Europe promoted similar faunas, in contrast to the subequatorial paleolatitudinal position of known North American fossil occurrences in Texas, New Mexico, and Arizona; (2) at that time, the geographical distance between Greenland and central Europe was shorter than to southern North America, which may have facilitated dispersal; and (3) the deserts and arid regions separating Greenland and Texas, New Mexico, and Arizona may have been a much more efficient barrier to the temnospondyls than the proto-Atlantic between Greenland and Europe. Some tolerance for salinity may have given a dispersal advantage to capitosauroids.

Conclusions

Cyclotosaurus naraserluki is the largest amphibian ever reported from Greenland. It possesses several autapomorphies that distinguish it from its sister taxon, *C. mordax*, within the genus *Cyclotosaurus*.

The record of *Cyclotosaurus* from the Fleming Fjord Formation in East Greenland, together with *Gerrothorax pulcherrimus*, shows a close correlation between the Greenlandic Late Triassic amphibian fauna and the amphibian fauna of the coeval European basins, such as Germany, Poland, and Portugal.

The temnospondyl faunas of Europe and the Scandinavian Arctic (Greenland and Svalbard archipelagos) are characterized by taxa not found in coeval temnospondyl faunas from North America, showing a geographical connection between East Greenland and central Europe despite the opening of the North Atlantic.

The geographic position of Greenland and the Jameson Land Basin during the Late Triassic makes *C. naraserluki* one of the amphibians known to have lived at the highest paleolatitude, sharing trophic habitats with other amphibian and reptilian predators.

CHAPTER 4 - A NEW TYPOTHORACINE AETOSAUR (ARCHOSAURIA: AETOSAURINAE) FROM THE LATE TRIASSIC FLEMING FJORD FORMATION OF GREENLAND

Abstract

The Late Triassic (Norian-early Rhaetian) Fleming Fjord Formation, cropping out at the Jameson Land Basin in East Greenland, bears a rich fossil vertebrate fauna that includes all the major clade present at that time on Earth. Aetosaur material had previously been reported from this formation and ascribed to two different stagonolepid taxa: *Aetosaurus ferratus* and *Paratypothorax andressorum*. However, a more detailed study on the material reported as *A. ferratus* allows us to hereby present *Sikuqisik jenkinsi* gen. et sp. nov., a new taxon endemic of East Greenland, with a likey age around 209–208 Ma. *S. jenkinsi* not only differs from *A. ferratus*, but its phylogenetic position encloses it to the most inclusive clade of the Typothoracinae. Its closest taxon within the Typothoracinae is *Apachesuchus heckerti*, from the early Rhaetian of New Mexico. The Typothoracinae are equally distributed between Europe, Greenland, and Southern USA, spanning from early Norian to early Rhaetian, with exception with *Aetobarbakinoidfes brasiliensis*, the only late Carnian taxon recorded from South America.

Introduction

Aetosauria were Late Triassic extensively-armored herbivorous archosaurs with an abundant fossil record from every modern continent except Oceania and Antarctica. Interrelationships among the aetosaurs are not well understood but two clades are properly recognized, with relatively apomorphic armours: the spinose Desmatosuchinae and the wide-bodied Aetosaurinae (see Parker 2007, 2016; Desojo et al. 2013; Schoch & Desojo 2016; Hoffman et al. 2018). Numerous expeditions by Harvard University to the Jameson Land Basin in central East Greenland from the late 1980's to the early 2000's reported at least two different taxa of aetosaurins from the Late Triassic Fleming Fjord Formation (Jenkins et al. 1994; Marzola et al. 2018).

Based on their large size and the dorsal ornamentation, one paramedian and two lateral dermal armor scutes from a large individual were ascribed by Jenkins *et al.* (1994, p. 13, fig. 10) to *Paratypothorax andressi* Long & Ballew 1985. Though no further study has been made on this specimen ever since, Parker (2016, p. 21) points out that: "*Although the specimen clearly possesses a raised anterior bar, radial pattern of pits and grooves, a dorsal eminence that contacts the posterior osteoderm margin, characteristic for paratypothoracins, the beveled posterior edge delineated by a distinct ridge is not a clear autapomorphy of* Paratypothorax andressorum *and thus this specimen should be assigned to Paratypothoracini*".

A more complete specimen, represented by both cranial and post-cranial material, was ascribed by Jenkins *et al*. (1994, p. 12–13, figs. 8–9) to *Aetosaurus ferratus* Fraas 1877, based on *"[...] 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"* as well as on the ornamentation of the dermal scutes. Later studies reported this specimen such as *Aetosaurus* (see Schoch 2007) or as *A. ferratus* (see Parker 2016; Marzola et al. 2018). However, Parker (2014, p. 375) indicates that the Greenland material may represents an undiagnostic aetosaurin in need of a detailed apomorphy-based revision.

Here we present a detailed anatomical description and phylogenetic context of *Sikuqisik jenkinsi* gen. et sp. nov., a new Late Triassic typothoracine aetosaur of East Greenland (Fleming Fjord Formation, Jameson Land Basin) previously reported as *Aetosurus ferratus*. *S. jenkinsi* is unique among Aetosaurinae because of two autapomorphies on the dorsal vertebrae and a unique combination of two characters (one cranial and one on axial skeleton). Typothoracinae ranges from the Late Carnian to the early Rhaetian and are reported also with at least six taxa from Southern USA, two from Germany, and one from Brazil.

Geological Settings

The Late Triassic (Norian–early Rhaetian) Fleming Fjord Formation of the Jameson Land Basin of central East Greenland (Fig. 4.1a) is composed of lacustrine and fluvial deposits rich in vertebrate remains (see Clemmensen 1980a, 1980b; Clemmensen et al. 1998, 2016; Marzola et al. 2018). During the Late Triassic, the Jameson Land Basin laid at about 40º N (Kent and Clemmensen 1996; Kent and Tauxe 2005), or in a climatic transition zone between the relatively dry interior of the supercontinent

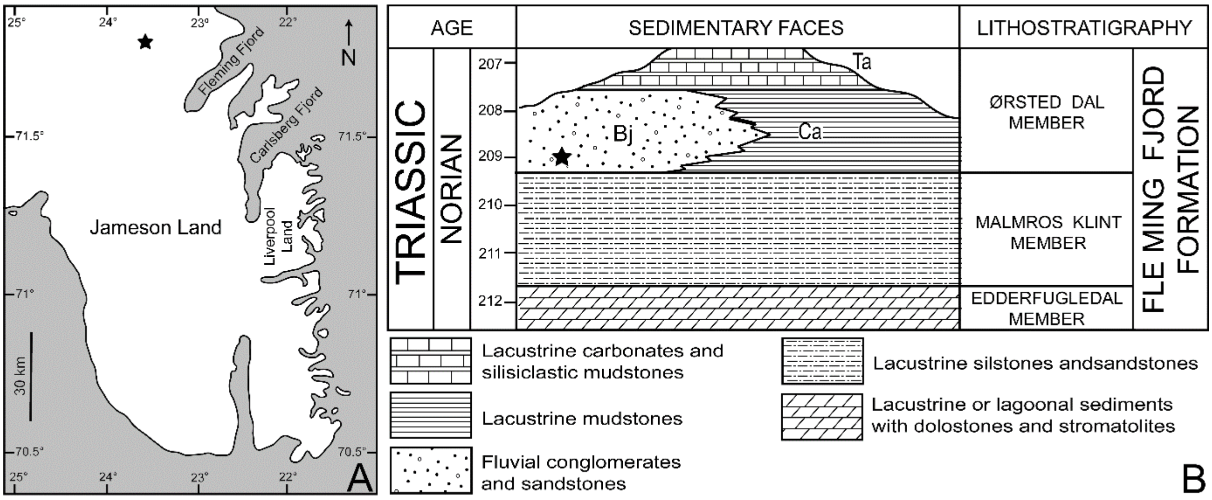

Figure 4.1 - A, geographical map of the Jameson Land area of East Greenland; B, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al. 1998). Stars indicate the locality and the stratigraphic position of the aetosaur remains. Abbreviations: **Bj**, Bjergkronerne beds; **Ca**, Carlsberg Fjord beds; **Ta**, Tait Bjerg Beds

Pangaea and the more humid peripheral part of this continent (Clemmensen et al. 1998; Sellwood and Valdes 2006; Kent et al. 2014).

The Fleming Fjord Formation is subdivided into a lowermost Edderfugledal Member, a middle Malmros Klint Member and an uppermost Ørsted Dal Member (Clemmensen 1980b). While the two lowermost members are lacustrine in origin and show little variation in lithology across the basin, the Ørsted Dal Member is characterized by marked changes in lithology both laterally and vertically (Jenkins et al. 1994; Clemmensen et al. 1998). In the eastern part of the basin, this member is initiated by red lacustrine mudstones and thin wave-rippled silt- and sandstones (Carlsberg fjord beds) that are overlain by variegated lacustrine mudstones and dolomitic limestones (Tait Bjerg Beds). In the western part of the basin, the lowermost part of the Ørsted Dal Member is composed of fluvial conglomerates and pebbly sandstones with subordinate mudstones (Bjergkronerne beds); these sediments are overlain by lacustrine deposit of the Tait Bjerg Beds (Jenkins et al. 1994; Clemmensen et al. 1998; Fig. 4.1b).

Based on the astrochronostratigraphic polarity time scale, Kent *et al.* (2017) suggested that Norian spans from 227 Ma to 205.5 Ma, though the latest version of the International Chronostratigraphic Chart (available at http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.pdf) sets the Norian/Rhaetian boundary at 208.5 Ma. The Ørsted Dal member of the Fleming Formation was tentatively given a Norian age by Clemmensen (1980b). Kent and Clemmensen (1996) and Clemmensen et al. (1998) suggested two possible age estimates, based on magnetochronology. The preferred model places the Ørsted Dal Member between ~209 Ma and ~207 Ma, giving a late Norian–early Rhaetian age for the member. The second estimate, places the Ørsted Dal Member between ~215 to ~213 Ma, corresponding to a mid-late Norian age. Andrew *et al.* (2014) suggested that the member has an age between 218 and 206 Ma giving a Norian–early Rhaetian for the member. Bjergkronerne beds, in which the new fossil was found, belong to the basal part of the Ørsted Dal Member; therefore, this bed unit would be of latest Norian age, according to Kent and Clemmensen (1996), Clemmensen *et al.* (1998), and Kent et al. (2017).

The material described in this study was found in a river channel sandstone in the middle part of the Bjergkronerne beds at Sydkronen (western part of the basin). The channel sandstone has a thickness of about 1 m and the bone remains were placed in the middle and central part of the channel sandstone body. The rivers that formed the Bjergkronerne beds drained a western upland and delivered sediment to the lake in the central and eastern part of the basin.

Material and Methods

The studied material is deposited at the Natural History Museum of Denmark (Copenhagen) as NHMD 190375, a dorsal paramedial osteoderm preserved as natural imprint of the dorsal surface; NHMD 190376, nearly complete skull missing the tip of the snout, anteriorly to the antorbital fenestra; NHMD 190377, articulated caudal paramedian and lateral osteoderms mostly preserved as natural imprint;

NHMD 190378, block containing a left femur and several dorsal osteoderms; and NHMD 190379, four articulated dorsal vertebrae (Figs. 4.2–4.6). Supposedly, all the specimens abovementioned belong to one individual. The first specimen found, NHMD 190379 (field number 74/91G) was collected in 1991, between August 12th and 18th, by William W. Amaral, Neil Shubin and one of us (LBC), during the 1991 Harvard University Vertebrate Paleontological Expedition to Jameson Land (East Greenland). On the following year expedition, the rest of the material (field number MCZ 22/92G), including the holotype, was collected by William W. Amaral and Farish A. Jenkins between July 14th and 17th 1992. Final preparation of NHMD 190377–79 has been made by one of us (MM) at the Lab facilities of the Museu da Lourinhã (Portugal) during February 2018. All the reported specimens are currently in exhibition at the GeoCenter Møns Klint (Denmark).

3D model of the skull NHMD 190376 has been made through photogrammetry (see Mallison & Wings 2014), using AgiSoft 1.2.0. 1M-face models are available in the Supplementary Material (S4.1). The description of the anatomy of the vertebrae follows the proposed nomenclature in Tschopp (2016).

Phylogenetic analysis

Phylogenetic analysis was performed with TNT 1.5-beta was used (available at www.lillo.org.ar/phylogeny/tnt; see Goloboff and Catalano 2016). *Sikuqisik jenkinsi* was initially coded in the data set by Parker (2016) for a total of 29 taxa and 83 characters, ten of which ordered (ch. 3, 4, 14, 22, 64, 70, 73, 76, 79, and 83; Parker, pers. comm. 2018) (Appendix A2). We performed 1000 replications using Wagner trees, followed by tree-bisection-reconstruction (TBR), retaining 10 trees per replication.

However, as reported for the analysis in Parker (2016), the strict consensus tree obtained shows a large polytomy given by *Aetobarbakinoides brasiliensis* Desojo et al. 2012. Therein, we also pruned of *A. brasiliensis* from our analysis, obtaining a matrix of 28 taxa and 83 characters.

Systematic Paleontology

DIAPSIDA Osborn 1903
ARCHOSAURIA Cope 1869
SUCHIA Krebs 1974
AETOSAURIA Marsh 1884
STAGONOLEPIDIDAE Lydekker 1887
TYPOTHORACISINAE Parker 2007 (alternative junior spelling: TYPOTHORACINAE)
Genus *SIKUQISIK* nov.

LSID. Not registered yet.

Type and only known species. *Sikuqisik jenkinsi* sp. nov.

Derivation of name. *Sikuqisik* is a combination of 'siku' and 'quisik', Greenlandic for, respectively, 'ice' and 'skin'.

Diagnosis. As for species.

Sikuqisik jenkinsi sp. nov.

Figures 4.2–4.7

1994 *Aetosaurus ferratus* Fraas 1877; Jenkins et al. pp 12–13, figs. 8–9

2007 *Aetosaurus* Fraas 1877; Schoch, p. 13

2016 *A. ferratus*; Parker, p. 11

2018 *A. ferratus*; Marzola et al., p 32, fig. 13B

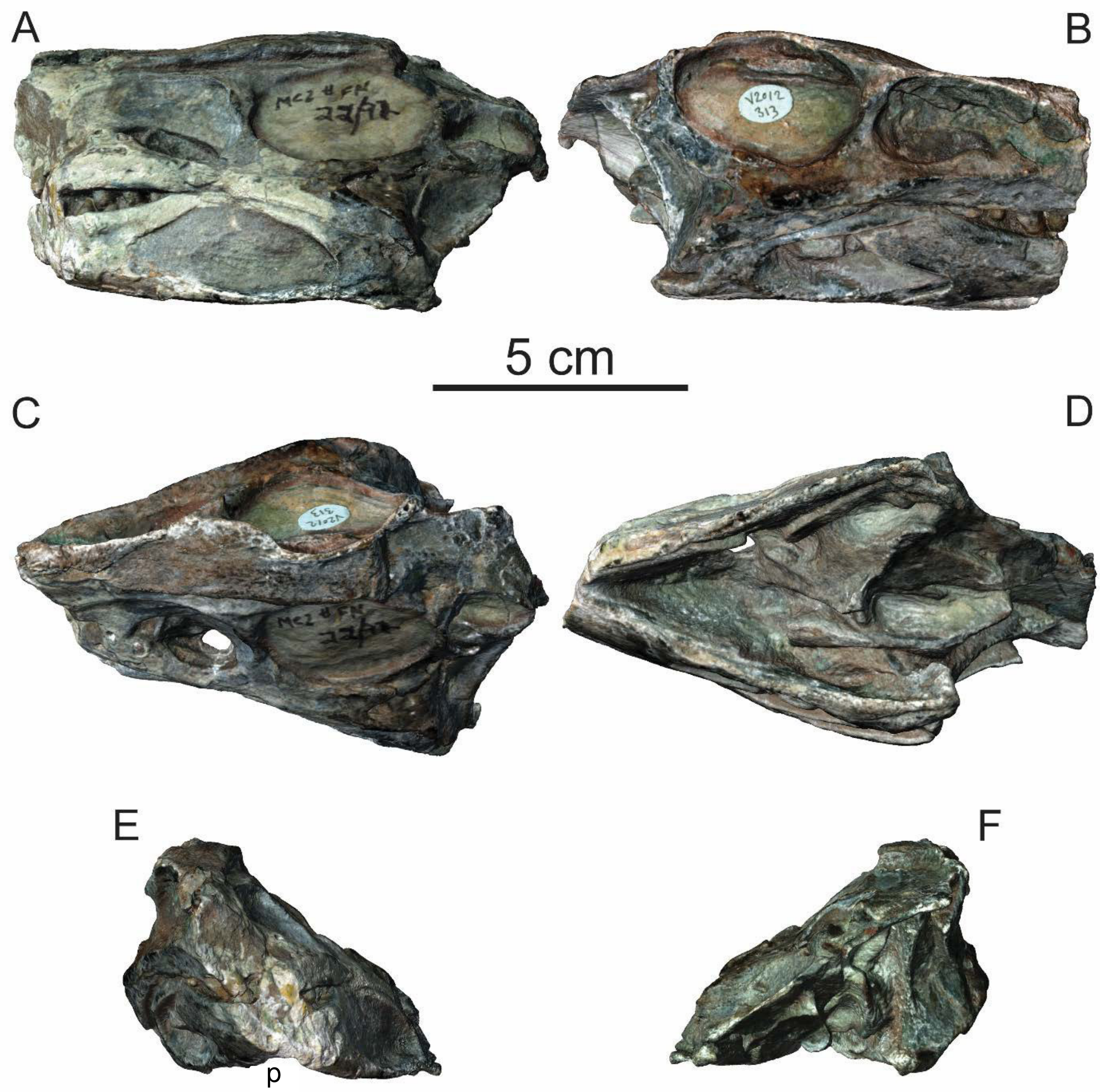

Figure 4.2 - *Sikuqisik jenkinsi* gen. et sp. nov.: skull NHMD 190376. A, lateral left; B, lateral right; C, dorsal; D, ventral; E, frontal; and F, posterior orthogonal views obtained by the photogrammetric model.

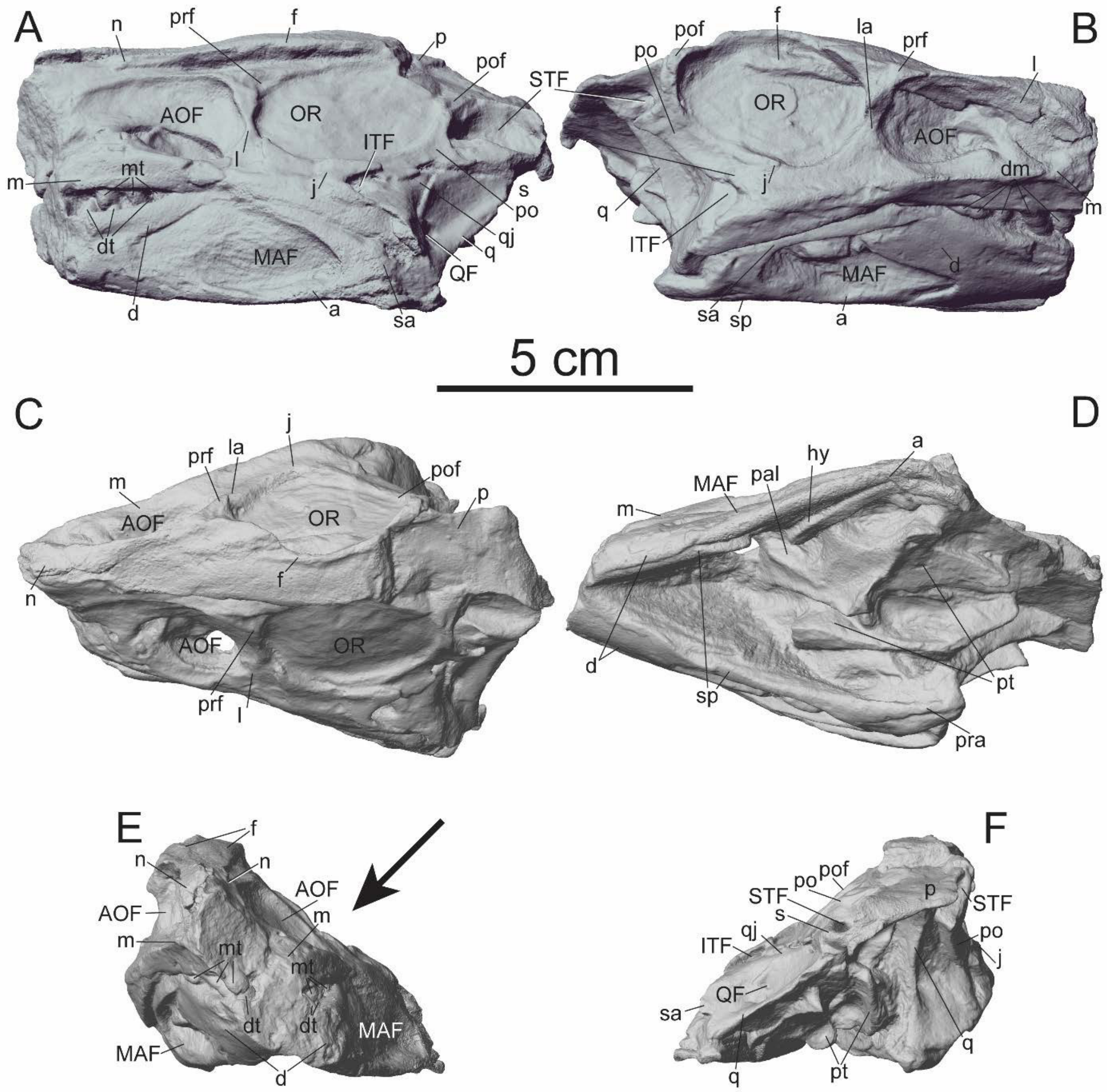

Figure 4.3 - *Sikuqisik jenkinsi* gen. et sp. nov.: skull NHMD 190376. A, lateral left; B, lateral right; C, dorsal; D, ventral; E, frontal; and F, posterior orthogonal views obtained by the photogrammetric model ventral orthogonal views in solid color, obtained by the photogrammetric model. The arrow in E shows the perspective from which the drawing in Fig. 4.4 was taken. Abbreviations: **a**, articular; **AOF**, antorbital fenestra; **d**, dentary; dt, dentary tooth; **f**, frontal; **hy**, hyoid; **ITF**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **m**, maxilla; **MAF**, mandibular fenestra; **mt**, maxillary tooth; **n**, nasal; **OR**, orbit; **p**, parietal; **pa**, palatine; **po**, postorbital; **pof**, postfrontal; **pra**, prearticular; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **QF**, quadrate foramen; **qj**, quadratojugal; **s**, squamosal; **sa**, surangular; **sp**, splenial; **STF**, supratemporal fenestra.

LSID. Not registered yet.

Holotype. One individual composed by NHMD 190376 (former field number V-2012-313), an articulated skull lacking the anterior part of the snout (Figs. 4.2–4.4; S4.1); NHMD 190375 (former V-2012-288), natural imprint of the dorsal surface of a dorsal paramedial osteoderm (Fig. 4.6G); NHMD 190377 (former V-2012-315a), natural cast of the dorsal surface of an articulated sequence of ventral paramedian and lateral caudal osteoderms (Fig. 4.7); NHMD 190378 (former V-2012-324a-b), a block containing a left femur, at least four dorsal osteoderms and unidentified bone fragments (Fig. 4.6A–F); NHMD 190379 (former V-2012-332), a sequence of four articulated dorsal vertebrae (Fig. 4.5).

Derivation of name. In honor of Prof. Farish A. Jenkins Jr. (1940–2012), leader of previous expeditions to East Greenland and discoverer of many Greenlandic vertebrates.

Type Locality. All the above-mentioned specimens were found at locality Sydkronen, at the western part of the Jameson Land Basin (East Greenland - 71º50.416'N, 23º39.281'W).

*Type Horizon***.** Fluvial channel deposits in the middle part of the Bjergkronerne beds (lowermost unit of the Late Triassic Ørsted Dal Member), approximately 150 m below the top of the member (Fig. 4.1).

Diagnosis. *Sikuqisik jenkinsi* belongs to the clade of the Typothoracisinae by sharing one of the six synapomorphies given by Parker (2007), or that its transverse processes of the dorsal vertebrae are elongate, more than twice as wide as the centrum. *S. jenkinsi* is unique among the Typotoracisinae for having the ventral margin of the jugal posteroventrally inclined in lateral view. Moreover, *S. jenkinsi* presents two new autapomorphies in its dorsal vertebrae: (1) the neural spine attaches to the posterior part of the centrum and its inclined anteriorly; and (2) the posterior rim of the dorsal transverse processes being irregular, narrowing around its mid length with one to two sub-rectangle indentations.

Description

Cranial skeleton

Upper skull and mandibles. NHMD 190376 (Figs. 4.2–4.4, S4.1) is a skull that preserves both the upper part and the two lower mandibles, but that misses the anteriormost part of the snout, being cut transversely about the anterior rim of the antorbital fossa. The right and left side are considerably deformed to one another, where the left side projects more ventrally in axial view. The overall preservation of NHMD 190376 is good, but the main bone sutures and contact are weak, making it overall hard and in often impossible to identify bone-to-bone contacts.

The antorbital fenestra is oval and elongated anteroposteriorly, 33 mm long and 23 mm wide. It is rimmed anteriorly and ventrally by the maxilla and by the lacrimal dorsally and posteriorly; in the dorsal part of the rim, the maxilla seems to form the anterior-most part of it, contacting the nasal around one third of the fossa length, so that the nasal projects into the antorbital fenestra rim, not allowing the contact between the maxilla and the prefrontal, which seems to slightly participate to the dorsolateral part of the rim. The orbit is the largest fenestra of the upper skull and it is sub-circular in shape, with a length of 35 mm and a width of 30 mm. It is bordered anteriorly by the lacrimal, antero-dorsally by the prefrontal, anteroventrally by the jugal, posteroventrally by the postorbital and posteriorly by the postorbital. The posterodorsal part of the orbit rim is allegedly made by the postfrontal, though how this bone contacts the surrounding parietal and postorbital is unclear. Posteriorly to the orbit there is the

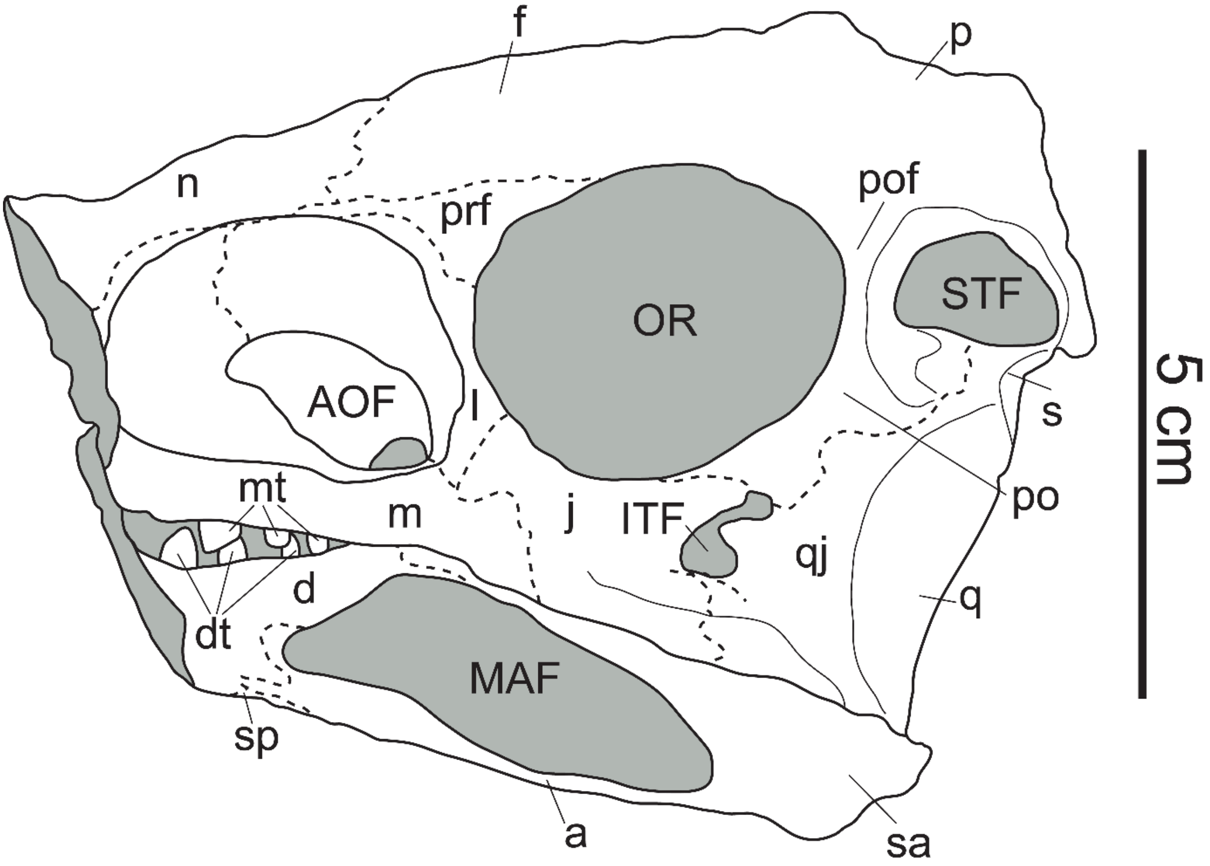

Figure 4.4 - *Sikuqisik jenkinsi* gen. et sp. nov.: an interpretative drawing of the left side from perspective perpendicular to the side plane (see arrow in Fig. 4.3E). Abbreviations: **a**, articular; **AOF**, antorbital fenestra; **d**, dentary; **dt**, dentary tooth; **f**, frontal; **ITF**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **m**, maxilla; **MAF**, mandibular fenestra; **mt**, maxillary tooth; **n**, nasal; **OR**, orbit; **p**, parietal; **pof**, postfrontal; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **s**, squamosal; **sa**, surangular; **sp**, splenial; **STF**, supratemporal fenestra

supratemporal fenestra, an oval hole, dorsoventrally compressed, 15 mm long and 10 mm wide. To its rim participate the postfrontal anteriorly, the parietal dorsally and the squamosal ventroposteriorly. Below the posterior-most part of the orbit, a small, circular cavity with a diameter of about 5 mm, the infratemporal fossa. The anterior part of its rim is made by a posterior projection of the jugal, that seems to contact the postorbital with a horizontal contact right below the orbit. The postorbital is hence involved in the rim of the infratemporal fossa, with the quadratojugal forming most of the posterior and dorsal part of the rim, where it contacts the jugal with a vertical contact below the fossa. Posteriorly to the infratemporal fossa, surrounded by the quadrate, a small quadrate foramen is noticeable in the right side of the upper skull. Part of the endocranium is weakly preserved, though in posterior and ventral views the pterygoid is appreciable.

The lower jaw is characterized by a large mandibular fenestra, 40 mm long and 17 mm wide. It is bordered anteriorly and anterodorsally by the dentary, anteroventrally and ventrally by the articular and posterodorsally and posteriorly by the surrangular. Lingually, part of the dorsal rim of the mandibular fenestra is made by the splenial. In ventral view, the posterior-most part of the lower jaw bears the prearticular, while the left hyoid bone seems to have been preserved dislocated to the lingual side of the left mandible.

Teeth. NHMD 190376 preserves at least 12 teeth, such as eight maxillary (five right, three left) and four from dentary (one right, three left). Their shape is conical, bulbous, with vertically straight tips, a sub-circular transversal section and slightly striated enamel.

Axial skeleton

Dorsal vertebrae. NHMD 190379 is a sequence of four dorsal vertebrae still in anatomical connection from anterior-medial position, probably corresponding to D3 to D6. The vertebrae are somewhat dorsoventrally compressed, with a slightly more accentuate deformation of the two most posterior ones. The centra are, in average, 15 mm long, 9 mm tall, and 8 mm width (Fig. 4.5). They have an hourglass shape in ventral view and are of the amphicoelous type. The neural arches attach to the centra on their posterior-most half and projects anteriorly. The neural arches in NHMD 190379 increase significantly in height from the most anterior (8 mm) to the most posterior vertebra (17 mm), though the dorsal-most part of the last two neural arches was reconstructed with a dark-grey epoxy resin during the first preparation of the specimen, in the 1990's. The neural arches have an overall squared shape in lateral view, being mediolaterally compressed and with a flat dorsal rim. Anteriorly, the neural arches connect to the vertebral centrum with an obtuse angle, so that, in lateral view, its attachment point to the centrum

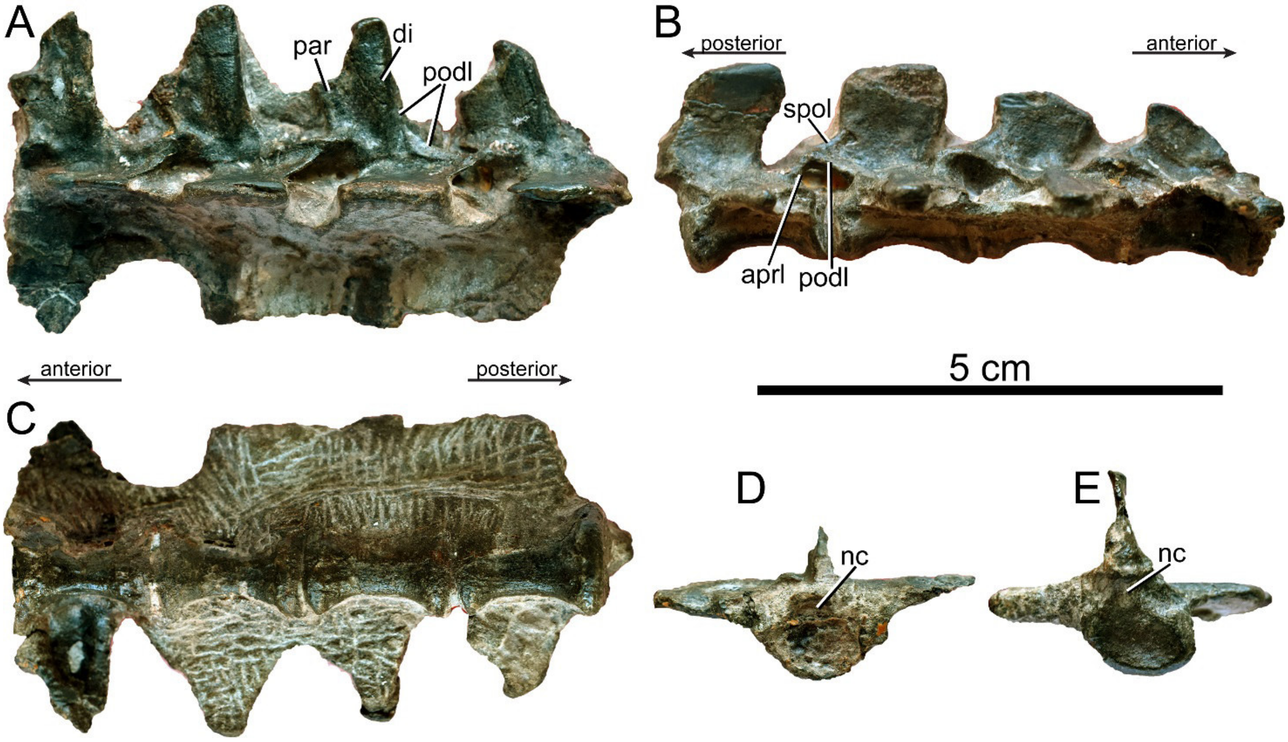

Figure 4.5 - *Sikuqisik jenkinsi* gen. et sp. nov.: sequence of the four dorsal vertebrae in anatomical connection NHMD 190379. A, dorsal; B, lateral right; C, ventral; D, anterior; and E, posterior orthogonal views. Abbreviations: **di**, diapophysis; **nc**, neural canal; **par**, parapophysis; **podl**, postzygadiapophyseal lamina; **prpl**, prezygaparapophyseal lamina; **spol**, spinopostzygapophysea lamina.

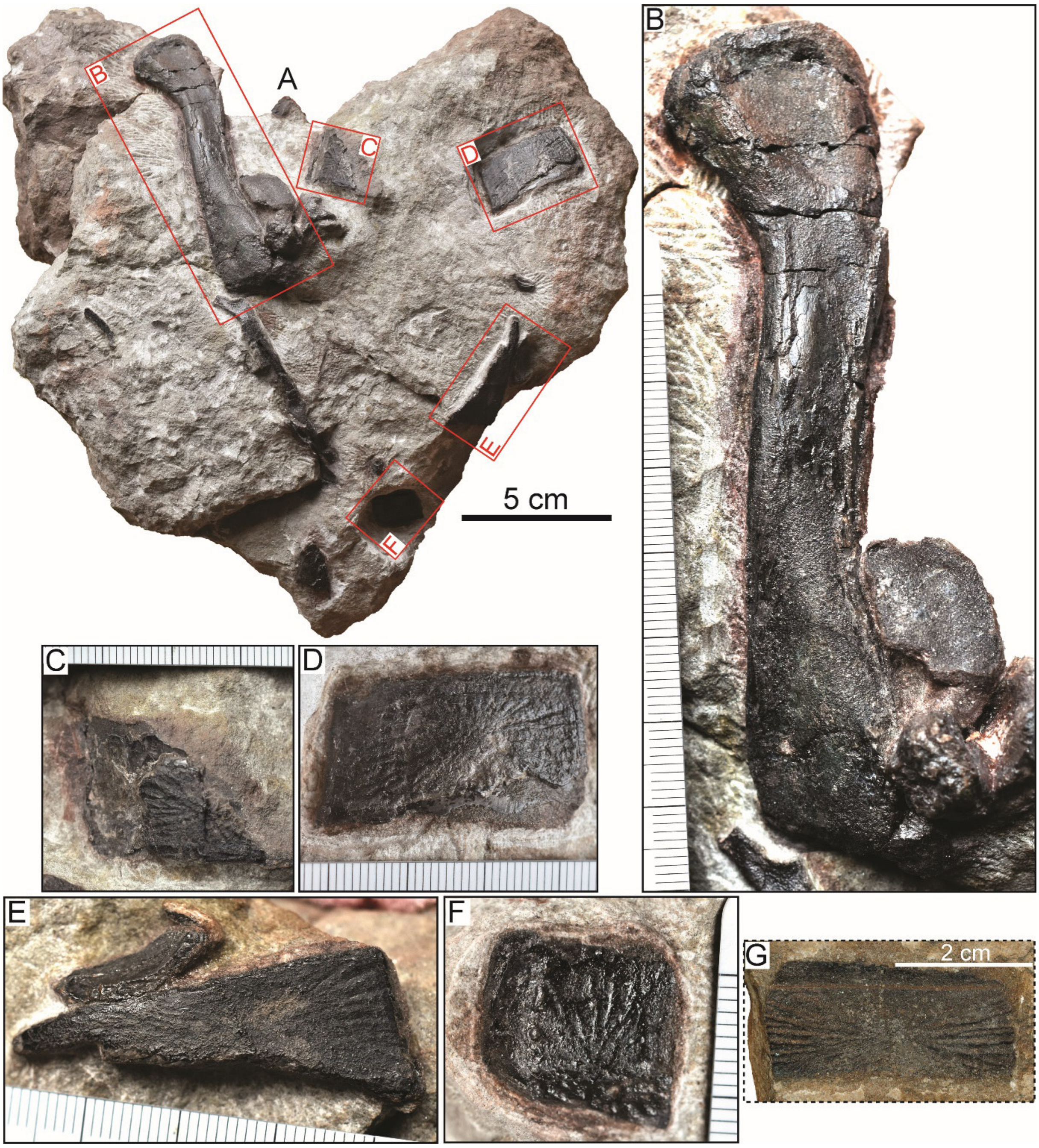

Figure 4.6 - *Sikuqisik jenkinsi* gen. et sp. nov.. A, block NHMD 190378 containing dorsal osteoderms and a left femur. B, close-up of the left femur; C–F, close-ups of four dermal osteoderms; G, natural imprint of the dorsal surface of the dorsal osteoderm NHMD 190375.

is more posterior than the dorsoanterior tip of the neural arch. Posteriorly, the neural arches connect to the postzygapophyses with two subtle, straight, blade-like spinopostzygapophyseal laminae (SPOL), that form an acute V-shape in dorsal view. The prezygapophyses are short and face anteriorly, while the postzygapophyses strongly project posteriorly, encountering the respective prezygapophyses above the anterior-most part of the centrum of the preceding vertebra. In *S. jenkinsi*, the parapophysis and

Figure 4.7 - *Sikuqisik jenkinsi* gen. et sp. nov.: sequence of ventral caudal osteoderms preserved as natural imprint of the dorsal (internal) surface, NHMD 190377.

diapophysis of every vertebra are fused between them, with the parapophysis always placed more anterior than the respective diapophysis.

Most of the lateral processes in NHMD 190379 are damaged; they generally lack the lateral tip or are partially covered with matrix. The only complete lateral process seems to be the right one of the second anterior-most vertebra, with a length of 17.5 mm. The lateral processes of *S. jenkinsi* are long, dorsoventrally compressed, with a blade-like anterior margin (parapophysis) that thicknesses to a strong and rounded posterior margin (diapophysis). In dorsal view, the anterior parapophyseal margin projects almost vertically, connecting to the prezygapophysis and forming the prezygaparapophyseal lamina (PRPL). The posterior diapophyseal margin slightly curves medially, due to the projection of the postzygadiapophyseal laminae (PODL). The anterior margin of the lateral processes presents an irregular rim, that expands anteriorly until about the mid length of the process, narrowing then abruptly with one to two sub-rectangle indentations where the parapophysis connects to the anterior rim of the diapophysis.

Paramedian dorsal osteoderms. Paramedian dorsal osteoderms can be identified in NHMD 190375 (Fig. 4.6g), a dorsal paramedial osteoderm preserved as natural imprint of the dorsal surface and at least four isolated osteoderms on the block NHMD 190378 (Figs. 4.6a, c–f). The average length and width of these paramedian dorsal osteoderms is, respectively, of 1.7 cm and 3.7 cm, though Jenkins et al. (1994, p. 13) stated that *“The scutes range up to 49 mm in transverse width and 20.9 mm in anteroposterior breadth; [...]”*. They apparently preserve a regular thickness all along the transverse section, with exception for the anterior articular surface, that thickens transversally, forming an anterior bar. There is no evidence of a proper center of ossification on any of the preserved osteoderms, though a couple of them (Figs. 4.6c, e) reveal a faint knob on the midline of their anterior margin, also showing a sort of midridge that runs anteroposteriorly. The ornamentation of the dorsal surface radiates from a central point with sub-straight ridges.

Paramedian and lateral caudal osteoderms. NHMD 190377 (Fig. 4.7) preserves the natural imprint of the dorsal surface of an articulated caudal paramedian and lateral osteoderms, with a few fragments of the original bones still noticeable. Due to their reduced size, we speculated that this sequence of osteoderms might be from the ventral part of the armor. Both the paramedial and the lateral osteoderms have an average length of 0.4 cm, with the formers having an average width of 1.0 cm and the latter of 0.5 cm. The paramedian osteoderms present a ridge running anteroposteriorly along their midline and ending, at the contact surface between two consecutive osteoderms, with a knob that projects ventrally. Such knob is also present on some of the lateral osteoderms, more in a medial position at the contact between two consecutive ones. The remaining portion of original bone, as well as some of the best-preserved impressions, show an irregular ventral surface, characterized by pits and ridges that seem to run transversally, slightly radiating from the center of every paramedian osteoderm.

Appendicular skeleton

Femur. NHMD 190378 comprehends a complete left femur (Figs. 4.6a–b). It is exposed only on its anterior surface and, partially, on sides. The anterior surface results slightly irregular, allowing to presume a partial collapse of the shaft and a slight anteroposterior flattening due to compression. Its overall aspect is elongated, slender, with a total length of 10.5 cm, a minimum shaft width of 1.2 cm and a maximum diaphyseal width of 2.3 cm. It bears a large, medially projected head, while both distal condyles are not perfectly appreciable, though the entire distal part looks rounded.

Phylogenetic Results

The first analysis led to nine most parsimonious trees, with a length (TL) of 209 steps, consistency index (CI) of 0.555, retention index (RI) of 0.732 and a rescaled consistency index (RCI) of 0.406. This analysis led to a large polytomy at the base of the tree (Fig. 4.8A) that, as also previously reported in Parker (2016), depended on *Aetobarbakinoides brasiliensis*.

The second analysis, performed with *a priori* pruned *A. brasiliensis*, gave one most parsimonious tree, with a TL of 207, CI of 0.560, RI of 0.738 and RCI of 0.413 (Figs. 4.8B, C). Bremer support and bootstraps values (1000 replicates) have been calculated and are reported in Fig. 4.8B.

Sikuqisik jenkinsi was recovered at the base of the Typothoracinae (=Typothoracisinae in Parker 2007), making a polytomy with *Apachesuchus heckerti* Spielmann & Lucas 2012 and the Paratypothoracini (=Paratypothoracisini in Parker 2007).

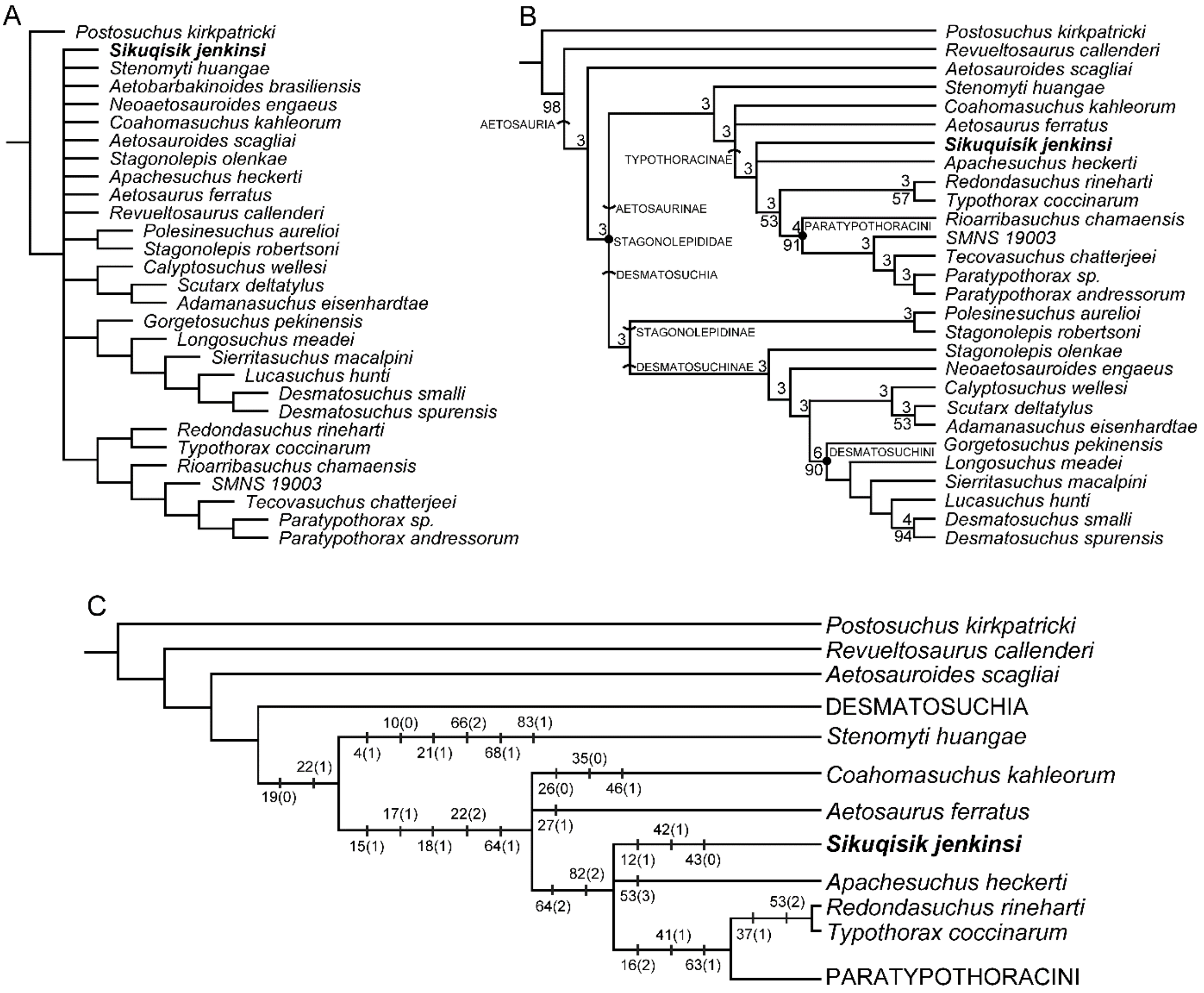

Figure 4.8 - Phylogenetic analysis. A, strict consensus tree of nine MPTs from the initial matrix produced by a TNT 1.5 analysis (29 taxa, 83 characters: TL of 203; CI of 0.552; RI of 0.730; RC of 0.403). B, reduced strict consensus of one parsimonious tree after a priori pruning of *Aetobarbakinoides brasiliensis* (28 taxa, 83 characters: TL of 208; CI of 0.558; RI of 0.736; RC of 0.410). Bremer support values higher than 1 (number over the branches) and bootstrap values after 1000 replicates higher than 50% (numbers under the branches) are shown. C, simplified reduced strict consensus tree (b). Full synapomorphies of non-paratypothoracini Aetosaruinae are shown along the branches and numbers refer to the characters listed in Parker (2016).

Discussion

Sikuqisik jenkinsi had been previously reported as *Aetosaurus ferratus* Fraas, 1877 (Jenkins et al. 1994; Schoch 2007; Parker 2016; Marzola et al. 2018). Though autapomorphies for *A. ferratus* slightly differ between the two most recent phylogenetic studies including this taxon (Schoch 2007; Parker 2016), *S. jenkinsi* has in common with *A. ferratus*: (1) a wide but short jugal, shorter in length than the orbit and that reaches only half the length of the maxilla; (2) a sub-rounded supratemporal fenestra, only one fifth the size of the orbit (because not properly specified, we interpret this character coded considering the superficial area of each fenestra); (3) a jugal transversally wider than long; (4) a quadratojugal indenting the infratemporal fenestra posteriorly; (5) an antorbital fossa that covers the majority of the lacrimal; (6)

dorsal paramedian plates 2 to 3.5 times wider than long. Our phylogenetic analysis recovered *S. jenkinsi* in a polytomy with *A. ferratus* and *Coahomasuchus kahleorum* Heckert and Lucas 1999. The two latter taxa share a nearly horizontal ventral margin of the jugal in lateral view (ch. 12-0) and short transverse processes of the dorsal vertebrae (ch. 40-0), while *S. jenkinsi* has a strongly inclined posteroventrally jugal (ch. 12-1, shared only with the Desmatosuchini *Desmatosuchus* Case 1920 and *Longosuchus meadei* Sawin 1947) and dorsal transverse processes twice as long as the dorsal centrum (ch. 40-1, unique among Aetosaurinae). *S. jenkinsi* differs from *A. ferratus* also by having the retroarticular articulation of the articular longer than high (ch. 32-1, shared with *Stenomyti huangae* Small & Martz 2013) and by lacking the supraorbitals (Schoch 2007). *S. jenkinsi* differs from *C. kahleorum* in addition by having bulbous maxillary teeth with straight tips in lateral views (ch. 35-2, shared with *A. ferratus*, *Typothorax coccinarum* Cope, 1875 and *S. huangae*) and an hyposphene-hypantrum articulation (ch. 43-0) in the dorsal vertebrae. A comparison between *S. jenkinsi* and its closest relative among the Typothoracinae, *Apachesuchus heckerti*, is somehow difficult, because the New Mexico taxon is represented in total by three paramedian osteoderms. Nevertheless, these two taxa differ by the pattern of the dorsal surface of their paramedian osteoderms, radiate in *S. jenkinsi* (ch. 53-1), smooth and flat in *A. heckerti* (ch. 53-3, unique among all Aetosauria).

We are confident to consider *S. jenkinsi* an adult individual, based on the fusion of the neural arches with the vertebral centra and, most of all, of the high degree of fusion between the skull bones which, in some case, are so extremely fused to make it very hard if not impossible to recognize the sutures.

The discovery of *S. jenkinsi*, a new typothoracinae aetosaur, not only increases the already wide variety of fossil vertebrates from the Fleming Fjord Formation, but it also adds to our knowledge on the paleobiogeography of the Late Triassic faunas. Among the Typothoracinae, the oldest known taxon is *Tecovasuchus chatterjeei* (223–221 Ma) from Southern USA, followed by *Paratypothorax* (222–210 Ma), from Germany, Greenland, and Southern USA, *Typothorax coccinarum* (218–206 Ma), from Southern USA, and the unnamed specimen SMSN 19003 (218–210 Ma) from Germany. *S. jenkinsi* has an age around 209–208 Ma. Its closest relative is *Apachesuchus heckerti*, from New Mexico, which however is younger in age (206–204 Ma) and coeval of *Redondasuchus rineharti*, from New Mexico. Overall, the distribution of the larger clade of the Aetosaurinae is confined to Europe, Greenland, and Southern USA, with only one taxon recovered from Southern America (*Aetobarbakinoides brasiliensis*) and seems to span from the late Carnian (~231 Ma) to the early Rhaetian (~204 Ma).

CHAPTER 5 - THREE OF THE OLDEST KNOWN TESTUDINATA AND THE DAWN OF TURTLES FROM THE LATE TRIASSIC OF THE FLEMING FJORD FORMATION (CENTRAL EAST GREENLAND)

Introduction

The origin and evolution of turtles are still two of the most fascinating, enigmatic, and discussed topics in vertebrate paleontology (Reisz and Laurin 1991; Lee 1996, 1997; Wilkinson et al. 1997; Joyce and Gauthier 2004; Reisz and Head 2008; Werneburg and Sánchez-Villagra 2009; Szczygielski 2015, 2017). In the last years, new species of Triassic stem- and basal turtles have been described (Rougier et al. 1995; Karl and Tichy 2000; Sterli et al. 2007; Li et al. 2008; Joyce et al. 2009; Schoch and Sues 2015; Szczygielski and Sulej 2016). Many studies also focused on the origin and the evolution of the turtle shell and skull (i.e., Nagashima et al. 2009; Joyce et al. 2009; Hirasawa et al. 2013; Bever et al. 2015; Szczygielski and Sulej 2018). Despite the origin of this clade is pointed by general consensus to the Late Triassic (see Rieppel and Reisz 1999; Benton 2014), up-to-date there are only a few known Late Triassic turtle taxa: *Chinlechelys* Joyce et al. 2009 from New Mexico, *Keuperotesta* Szczygielski and Sulej 2016 from Germany, *Odontochelys* Li et al. 2008 from China, *Palaeochersis* Rougier et al. 1995 from Argentina, *Proganochelys* Baur 1887 from Germany and Thailand, and *Proterochersis* Fraas 1913 from Germany and Poland (see also de Broin et al. 1982; de Broin 1984; Karl and Tichy 2000; Sulej et al. 2012; Szczygielski 2015; Szczygielski and Sulej 2016; Joyce 2017).

Moreover, some of the best-preserved specimens have not been yet subject of detailed anatomical descriptions, as well as of deepened phylogenetic analyses (Rougier et al. 1995; Karl and Tichy 2000; Li et al. 2008; Sterli et al. 2013; Schoch and Sues 2015). Also due to lack in properly described specimens, the phylogeny of basal turtles is often based mostly on the skull, carapace, and plastron (i.e., Lee 1996, 1997; Joyce 2007; Sterli and Joyce 2007; Sterli and de la Fuente 2013; Anquetin 2012); only a few characters are given for the axial skeleton, and even less are given for the appendicular skeleton (Joyce 2007; Joyce et al. 2013; Sterli and de la Fuente 2013).

A Late Triassic turtle has been briefly described from the Fleming Fjord Formation of the Jameson Land in East Greenland as cf. *Proganochelys* (Jenkins et al. 1994). Its affinity with *Proganochelys* was given based on the pairs of gular and intergular projections (Jenkins et al. 1994, p. 11). Nowadays, however, pairs of gular projections are also known in *Odontochelys* (see Li et al 2008, Fig. 1). Furthermore, the Greenlandic specimen in Jenkins et al. (1994) shares the dorsal epiplastral process both with *Odontochelys* and *Kayentachelys* Gaffney et al. 1987 (see Joyce 2007, p. 38, Fig. 11b), an Early Jurassic turtle from Arizona.

With this work, we aim (1) to present a complete and detailed anatomical description of NHMD Testudinata n. gen. et sp. gen. et. sp. nov., a new Late Triassic turtle from the Fleming Fjord

Formation of the Jameson Land Basin in East Greenland; (2) to frame this new basal turtle in a phylogenetic context; and (3) report first analyses made on two more Testudinata specimens from the Late Triassic of Greenland.

Geological Settings

The Late Triassic Fleming Fjord Formation (Clemmensen 1980a, 1980b) is well exposed in the Jameson Land Basin, nowadays located between 70° and 72° N in central East Greenland, corresponding to the land areas of Jameson Land and Scoresby Land. The basin was situated at the southern end of the East Greenland rift system, which formed part of a larger rift complex separating Greenland from Norway prior to the opening of the Atlantic (Ziegler 1988). It was bounded to the west by a major N–S trending fault and to the east by the Liverpool Land structural high. A possible NW-SE trending cross-fault in Kong Oscar Fjord defined the northern boundary of the basin. The southern boundary is unknown; however, the basin may have extended south of Scoresby Sund (Clemmensen 1980a; Surlyk 1990).

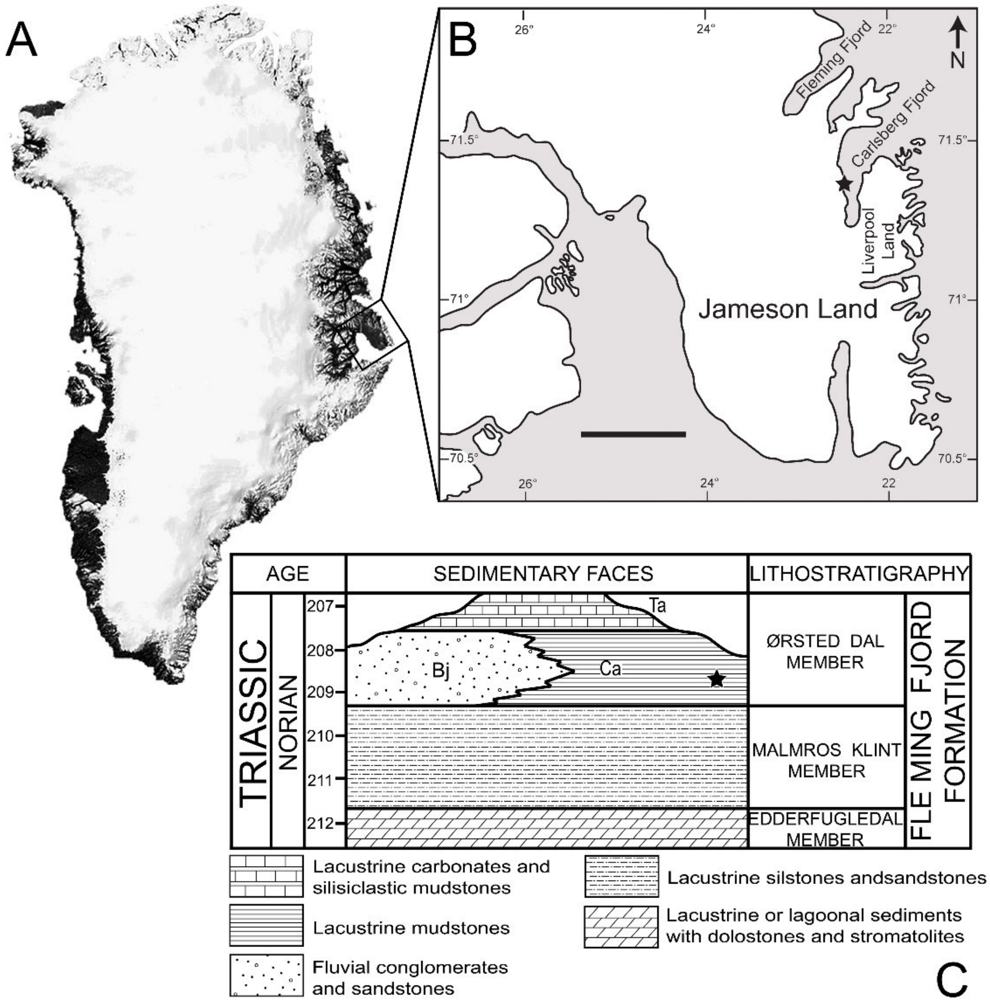

Figure 5.1. - A, geographical map of Greenland; B, close-up of Jameson Land and the Liverpool Land area; C, generalized stratigraphic scheme of the Fleming Fjord Formation (after Clemmensen et al. 1998). Stars in B and C indicate the site where the holotype of NHMD Testudinata n. gen. et sp. was discovered. Abbreviations: **Bj**, Bjergkronerne beds; **Ca**, Carlsberg Fjord beds; **Ta**, Tait Bjerg Beds. Scale bar equals 40 km (B).

During the Late Triassic, the Jameson Land Basin laid at 42° N (Kent and Clemmensen 1996; Kent and Tauxe 2005). This position placed the basin in a transition zone between the relatively dry interior of the supercontinent Pangaea and the more humid peripheral part of this continent (Clemmensen et al. 1998; Sellwood and Valdes 2006), or well inside the humid temperate belt (Kent et al. 2014).

The Late Triassic Fleming Fjord Formation is around 300 m thick in the central and eastern part of the basin (Clemmensen 1980a, 1980b; Jenkins et al. 1994). It is composed of cyclically bedded lacustrine deposits and is subdivided into 3 members: a lowermost Edderfugledal Member, a middle Malmros Klint Member, and an uppermost Ørsted Dal Member (Clemmensen et al. 1998; Clemmensen et al., in press). The latter member is divided into a unit of dominantly red mudstones (the Carlsberg Fjord beds) and an overlying unit of variegated mudstones and dolomitic limestones (the Tait Bjerg Beds). These deposits are in turn overlain by deltaic and lacustrine deposits of the Early Rhaetian-Sinemurian Kap Stewart Formation (Dam and Surlyk 1993). At most places, the boundary between these two formations is obscured by scree and solifluction deposits, with a clear unconformity at Lepidopteriselv site.

The Carlsberg Fjord beds are between 80 and 120 m thick and composed of siliciclastic sediments of mudflat and shallow lake origin. The succession is dominated by red-brown to purple massive mudstone; associated facies are intraformational conglomerates, light reddish or greenish-grey mud-peloid siltstone with wave-ripple cross-lamination, and light greyish, fine- to medium-grained sandstone with current-formed cross-stratification (Clemmensen et al. 1998). The upper surfaces of the wave-rippled siltstones carry frequent *Grallator* tracks (Clemmensen et al., 2016).

Sparse invertebrate fossils and land-derived palynomorphs suggest that the Carlsberg Fjord beds of the Ørsted Dal Member are of Norian to early Rhaetian age (Clemmensen 1980b), while paleomagnetic data give a narrower and more precise age estimate and suggest that the unit represents a time span of about 1.5 Myr around 208 Myr ago (Clemmensen et al. 1998). New evidence from high-precision U-Pb geochronology, places the Norian-Rhaetian boundary at about 205.5 Ma (Wotzlaw et al. 2014) suggesting that the Carlsberg Fjord beds are of latest Norian age.

Vertebrate fossils have consistently been reported from the Fleming Fjord Formation with most finds deriving from the Malmros Klint and Ørsted Dal Mbs. in the eastern part of the basin (Clemmensen 1980a; Jenkins et al. 1994, 1997, 2001, 2008; Shapiro & Jenkins. 2001; Mateus et al. 2014; Clemmensen et al. 2016; Marzola et al. 2017b, 2018; Agnolin et al. 2018). The remains of a turtle were found in the late 80s and briefly reported by Jenkins et al. (1994). The specimen was found in poorly exposed sediments in the upper part of the Carlsberg Fjord beds (Ørsted Dal Mb.) at Lepidopteriselv (71°15.760'N, 22°32.682'W, altitude: 285 m). A second specimen was found in 1995 at a mountain slope facing Ærenprisdal (71°32.611 N, 22°55.307 W, 580 m above sea level; data from

A8). This specimen was found in a red mudstone facies of the Carlsberg Fjord beds. Testudinata remains were also found in 2012 in poorly exposed Carlsberg Fjord beds at Wood Bjerg-Macknight Bjerg (71°22.965 N, 22°33.216 W; 462 m above sea level; Mateus et al. 2014; Clemmensen et al. 2016; Marzola et al. 2018).

Material and methods

The original material ascribed to NHMD Testudinata n. gen. et sp. n. gen et sp. has been through different depository numeration, resulting in a quite complicated and not linear sequence of NHMD numbers that are given for each specimen along the description.

3D models of NHMD Testudinata n. gen. et sp. have been made through photogrammetry (see Mallison & Wings 2014), using AgiSoft 1.2.0. PLY models are available in the Supplementary Material (S5.1–5.10).

Phylogenetic analysis

Phylogenetic analysis was performed with TNT 1.5-beta was used (available at www.lillo.org.ar/phylogeny/tnt; see Goloboff and Catalano 2016). NHMD Testudinata n. gen. et sp. has been coded in the data set by Li et al. (2016) for a total of 53 taxa and 280 characters (Appendix A3). We performed 1000 replications using Wagner trees, followed by tree-bisection-reconstruction (TBR), retaining 10 trees per replication.

Systematic Paleontology

Testudinata Joyce et al. 2004
NHMD Testudinata n. gen. et sp.
(Figs. 5.2–5.20; S5.1–5.10)

Holotype – Partial postcranial skeleton including carapace (nuchal, peripherals, costals, vertebrals, and pleurals), plastron (epi-, ento-, hyo-, meso-, hipo-, and xiphiplastron), shoulder and pelvic girdles, forelimbs, and hindlimbs with depository numbers NHMD 163391–163417.

Horizon and material **–** The specimen was collected by William R. Downs III during the 1995 expedition at Stairmaster Quarry (71° 32 611' N - 22° 55.307' W, at an altitude of 579 m asl) in the Carlsberg Fjord beds (Ørsted Dal Mb.) of the Fleming Fjord Fm. at Jameson Land, Central East Greenland. On the specimen, Stephen Gatesy and Neil Shubin confirmed that *"...we are pretty certain it came from the top of the section East of Ærenprisdal, from near the top of the Fleming Fjord section..."* (pers. comm. 2017).

Diagnosis – NHMD Testudinata n. gen. et sp. is a stem Testudinata supported by the presence of a bony shell made of a plastron and a carapace and the scapulacoracoid triradiate in shape. Derived character to stem Testudinata is the reduction of costal ossification with the presence of costal fontanelles in the carapace. Distinguished autapomorphies are: (i) the scapulacoracoid misses the coracoid foramen; (ii) proximal radio-ulnar ligament process weakly projecting medially; (iii) radio-ulnar articulation strongly concave; (iv) ulna with no sigmoid crest evident; (v) popliteal fossa subcircular that does not reach the edge of the condylar articulation and distally surrounded by a ridge; (vi) tibial proximal articular facet with two concavities separated by a crest; and (vii) tibial shaft bearing a dorsal massive ridge. A dubious character is the lateral process of the humerus projecting medially

Description

The type specimen consists of a substantial part of postcranial skeleton. Lot of the collected material is represented by innumerous undiagnostic carapace and plastron fragments. The original unpublished "Preliminary report of the Museum of Comparative Zoology 1995 Vertebrate Paleontological Expedition to Jameson Land, East Greenland", signed by Prof. Farish A. Jenkins on October 25, 1995, denotes that *"Although recovered in situ, the specimen had to be removed in many pieces because of the fragmentation of the surrounding matrix"* (A9). The preservation varies from poor, regarding the

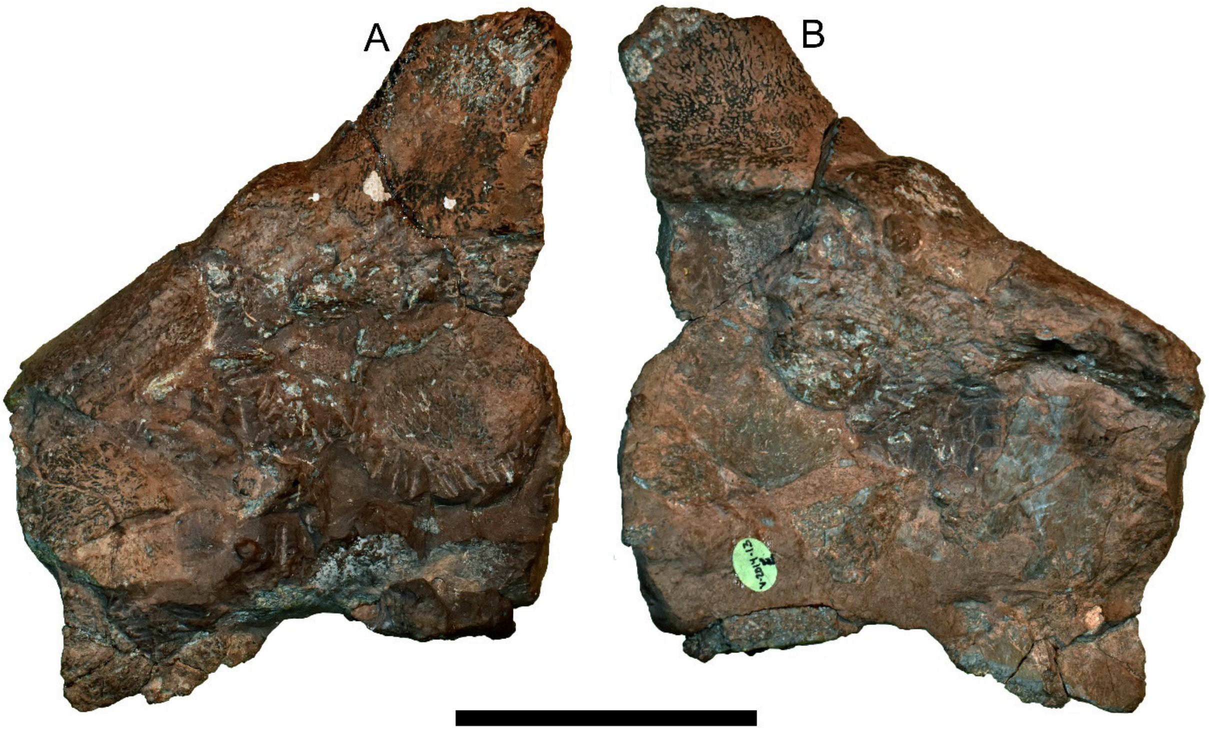

Figure 5.2 - NHMD Testudinata n. gen. et sp. holotype. Carapace fragment NHMD 163409 E. A, dorsal; B, ventral. Scale bar equals 5 cm.

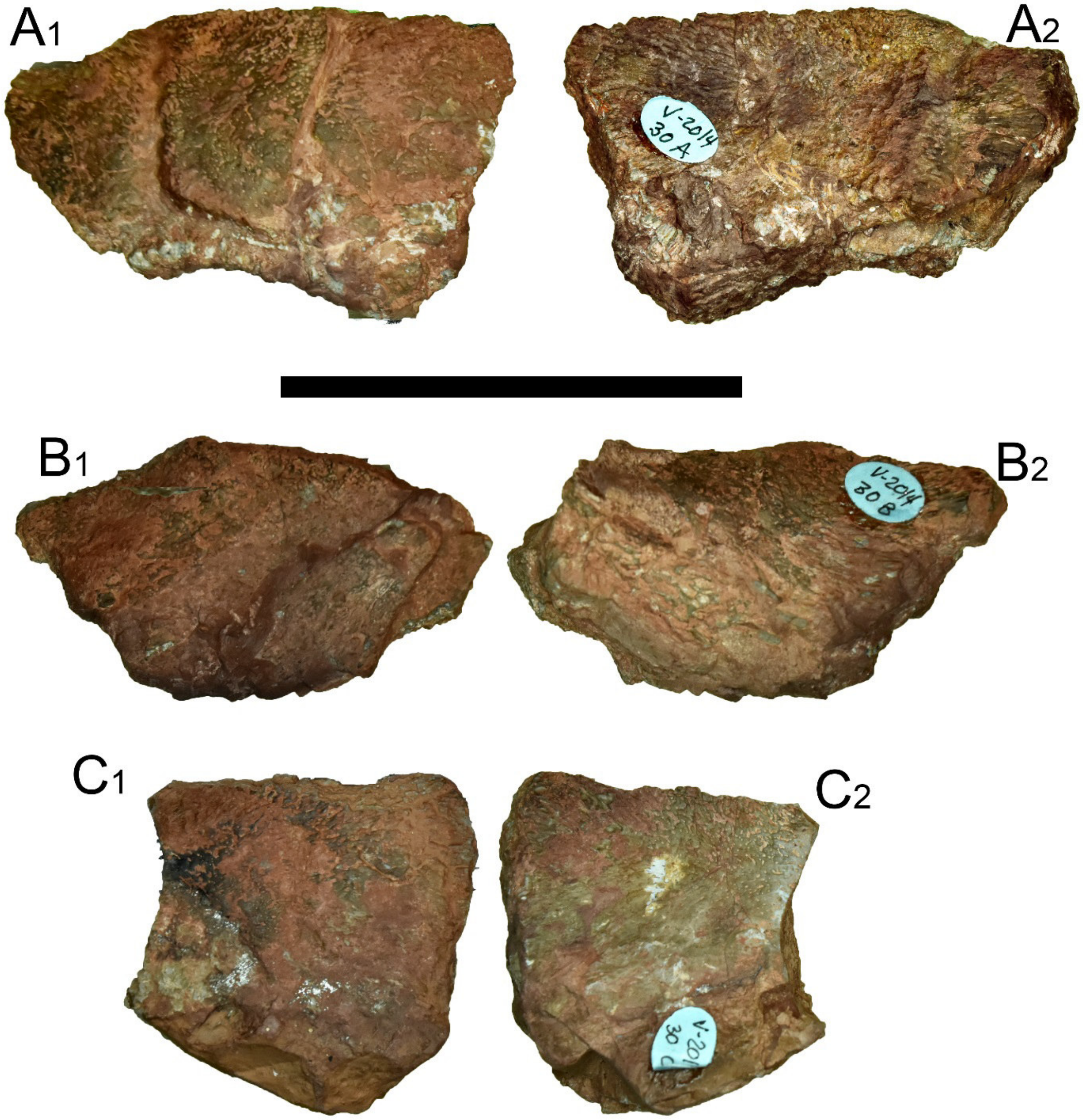

Figure 5.3 - NHMD Testudinata n. gen. et sp. holotype. Carapace, peripherals. A, NHMD 163398 A; B, NHMD 163398 B; C, NHMD 163398 C. Subscripts: 1, dorsal; 2, ventral. Scale bar equals 5 cm.

shell, to moderate to good regarding limbs and girdle bones. However, the entire specimen presents conspicuous taphonomic deformation that, somehow, seems to have affected more the left side.

Carapace

The most diagnostic carapace part is NHMD 163409 E, an element preserving part of the left nuchal, the left costal 1, and the first two left periferals (Fig. 5.2; S5.1). Scutes are not appreciable and, though most of the dorsal surface is covered in matrix, the nucal does not seem to bear any cervical scute. Dorsally, the preserved part of the nuchal has a sub-trapezoidal shape and it protrudes cranially. The contact with the first peripheral runs medially and it forms an embayment anteriorly. Peripheral 1 is

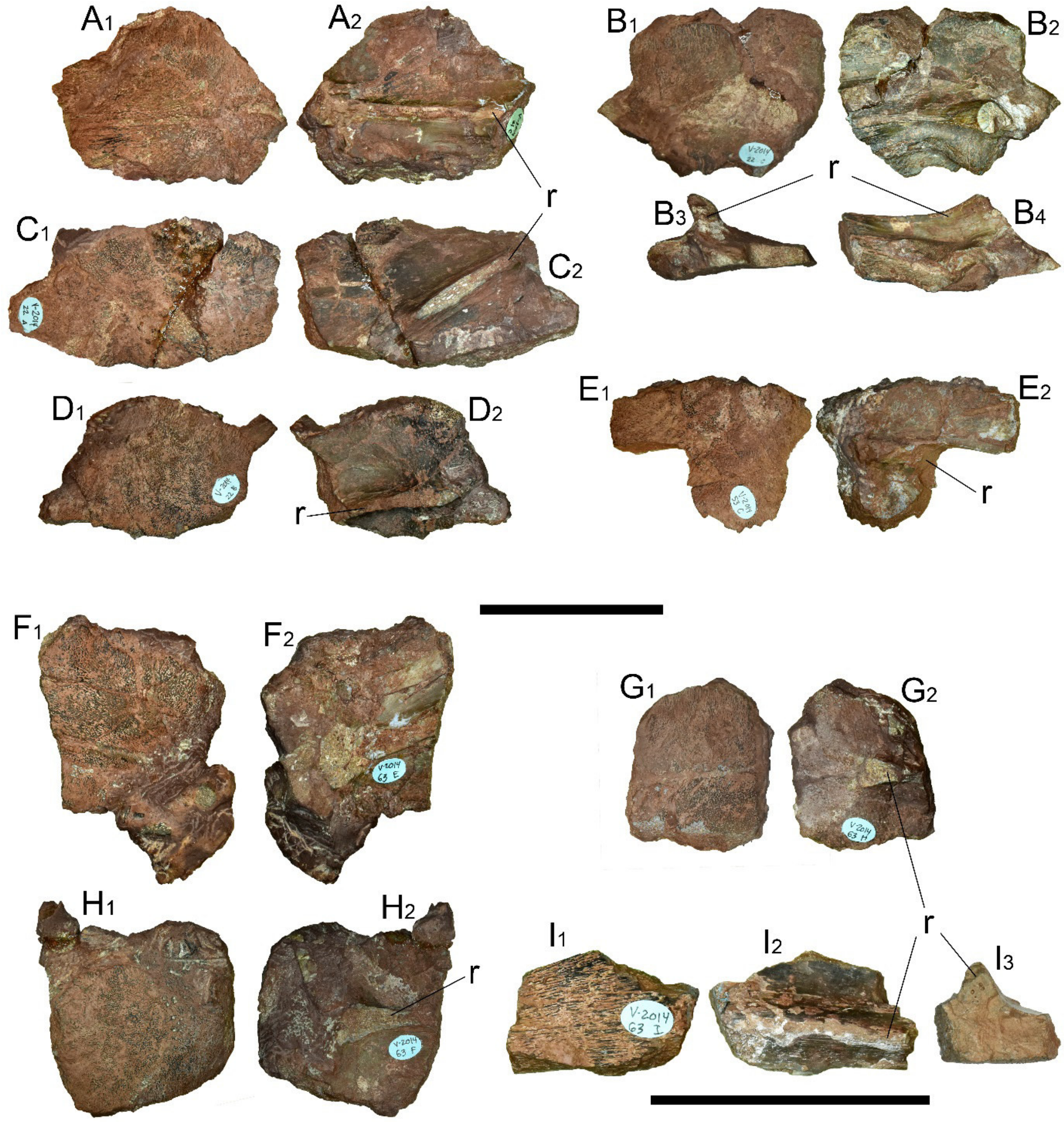

Figure 5.4 - NHMD Testudinata n. gen. et sp. holotype. Carapace, vertebrals. A, NHMD 163415 C; B, NHMD 163400 C; C, NHMD 163400 A; D, NHMD 163400 B; E, NHMD 163413 C; F, NHMD 163411 E; G, NHMD 163411 H; H, NHMD 163411 F; I, NHMD 163411 I. Subscripts: 1, dorsal; 2, ventral; 3, lateral; 4, frontal. Abbreviations: **r**, rib. Scale bar equals 5 cm.

smaller than peripheral 2, though the later looks not entirely preserved. The contact between the two peripherals is difficult to identify dorsally; nonetheless, it is clear in the anterior margin. Both peripherals 1 and 2 project ventrally, though this apparent projection might be mostly caused by the taphonomic deformation. In ventral view, the lower part of the nuchal presents a clear, distinct, U-shaped concavity, projecting laterally and that we interpret as the attachment for the left cleithrum.

NHMD 163398 A, B, and C are three peripheral elements that we speculate coming from the right anterior part of the carapace (Fig. 5.3). The radial section is sub-triangular, with the dorsal surface

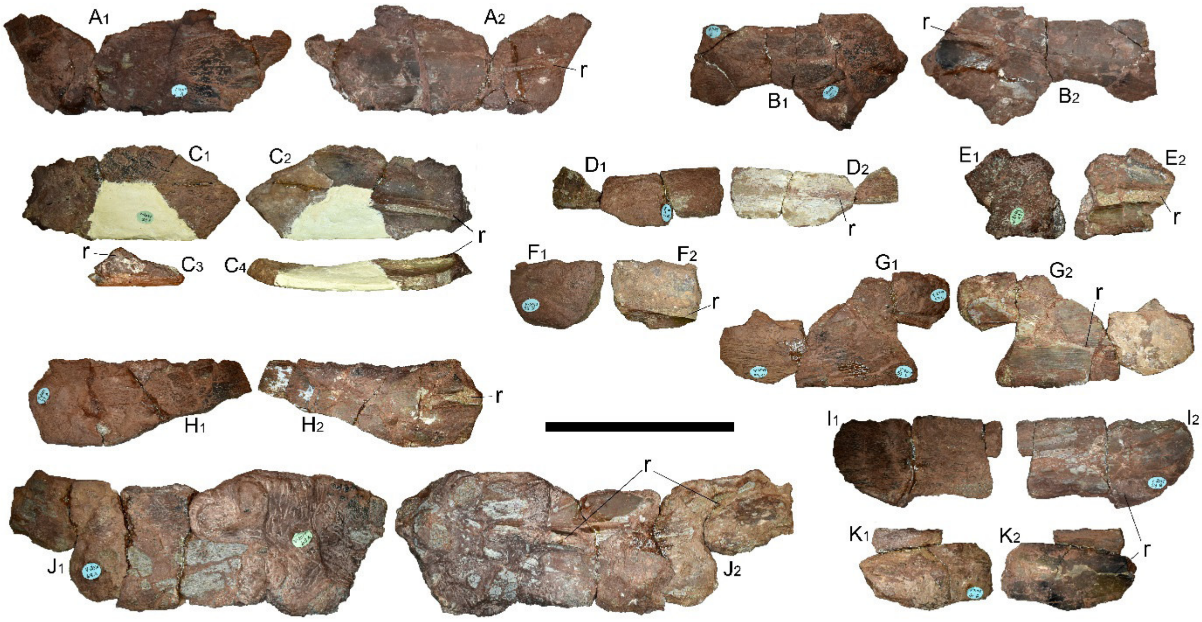

Figure 5.5 - NHMD Testudinata n. gen. et sp. holotype. Carapace, pleurals. A, NHMD 163415 A; B, NHMD 163400 D-E; C, NHMD 163392 E; D, NHMD 163417 B; E, NHMD 163391 J; F, NHMD 163413 B; G, NHMD 163413 L; H, NHMD 163413 A; I, NHMD 163411 B; J, NHMD 163411 A; K, NHMD 163411 G. Subscripts: 1, dorsal; 2, ventral; 3, lateral; 4, frontal. Light yellow parts were reconstructed during preparation. Abbreviations: **r**, rib. Scale bar equals 10 cm.

concave, the ventral surface convex, and the thickness decreasing laterally. We estimate NHMD Testudinata n. gen. et sp. to have a carapace length of 50–60 cm, after comparison with coeval genus *Proganochelys*.

At least 30 more fragments can be associated to NHMD Testudinata n. gen. et sp. carapace. The presence of dorsal ribs allows to describe the elements NHMD 163400 A–C, 163411 E-F-H-I, 163413 C, and 163415 C, as vertebral fragments (Fig. 5.4). The best-preserved element, NHMD 163415 C (Fig. 5.4A), shows a laminar rib fully fused to the costal, and projecting dorsoventrally. The anterior surface is slightly convex, while the posterior surface is strongly concave at the contact between the rib and the costal. The rib thickness is almost 1 cm medially and fades rapidly peripherally. Dorsally, the suture between two partial neurals and a costal can be identified. In NHMD Testudinata n. gen. et sp., the neurals appear to have a hexagonal shape, as also noticeable in other elements such as NHMD 163400 B (Fig. 5.4D).

Pleural elements NHMD 163391 J, 163392 E, 163400 D-E, 163411 A-B-G, 163413 A-B-L, 163415 A, and 163417 B (Fig. 5.5) are generally flat, slightly concave dorsally, with the dorsal surface somewhat irregular and the ventral surface smooth. Besides being partially reconstructed, NHMD 163392 E is the best pleural element in NHMD Testudinata n. gen. et sp. (Fig. 5.5C). The ventral surface presents a ridge that correspond to the peripheral ending of the rib. The rib orientation indicates this element to come from the left side of the carapace. The dorsal surface presents a partially preserved neural and two partially preserved costals. By consequence, each costal element of NHMD Testudinata n. gen. et sp. bears the rib very anteriorly, close to the suture with the following costal element. Despite

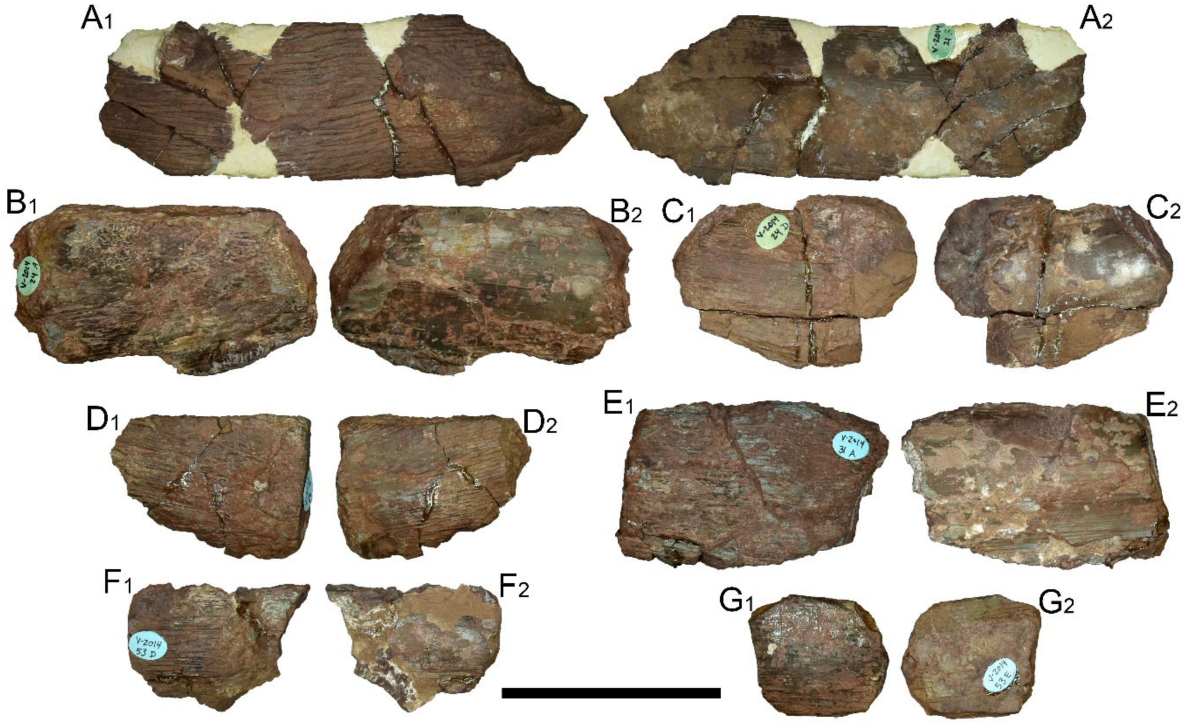

Figure 5.6 - NHMD Testudinata n. gen. et sp. holotype. Carapace, costals. A, NHMD 163415 C; B, NHMD 163392 A; C, NHMD 163392 D; D, NHMD 163404 B; E, NHMD 163417 A; F, NHMD 163413 D; G, NHMD 163413 E. Subscripts: 1, dorsal; 2, ventral. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

the incomplete reconstruction, two partial pleurals are preserved on the dorsal surface, separated by a deep, radial sulcus that runs radially over the neural element and along the suture between the two costals.

The elements NHMD 163392 A-D, 163410 B, 163413 D-E, 163415 B, and 163417 A are costals that we interpret as free rib ends (Fig. 5.6), based on the best preserved elemen NHMD 163415 B (Fig. 5.6A). Both lateral margins are complete and unfractured, indicating that no bony contact was made between two consecutive elements; the medial margin presents a fracture where it was originally attached to the rest of the costal element; the peripheral margin has an irregular, ventrally bumped surface, potentially indicating a contact with a marginal. In dorsal view, the element is slightly curve, with the anterior margin concave and the posterior margin convex. The element can be attributed to the right side of the carapace. The ventral surface is smooth, while the dorsal surface has a regular, linear pattern made of small ridges and depressions running medioperipherally. In anterior view, the element presents a sigmoid shape, probably due to taphonomic deformation. Though the carapacial remains allow the reconstruction of a complete sequence of two consecutive costals, free rib ends indicate the presence of fontanelles in the original specimen.

Plastron

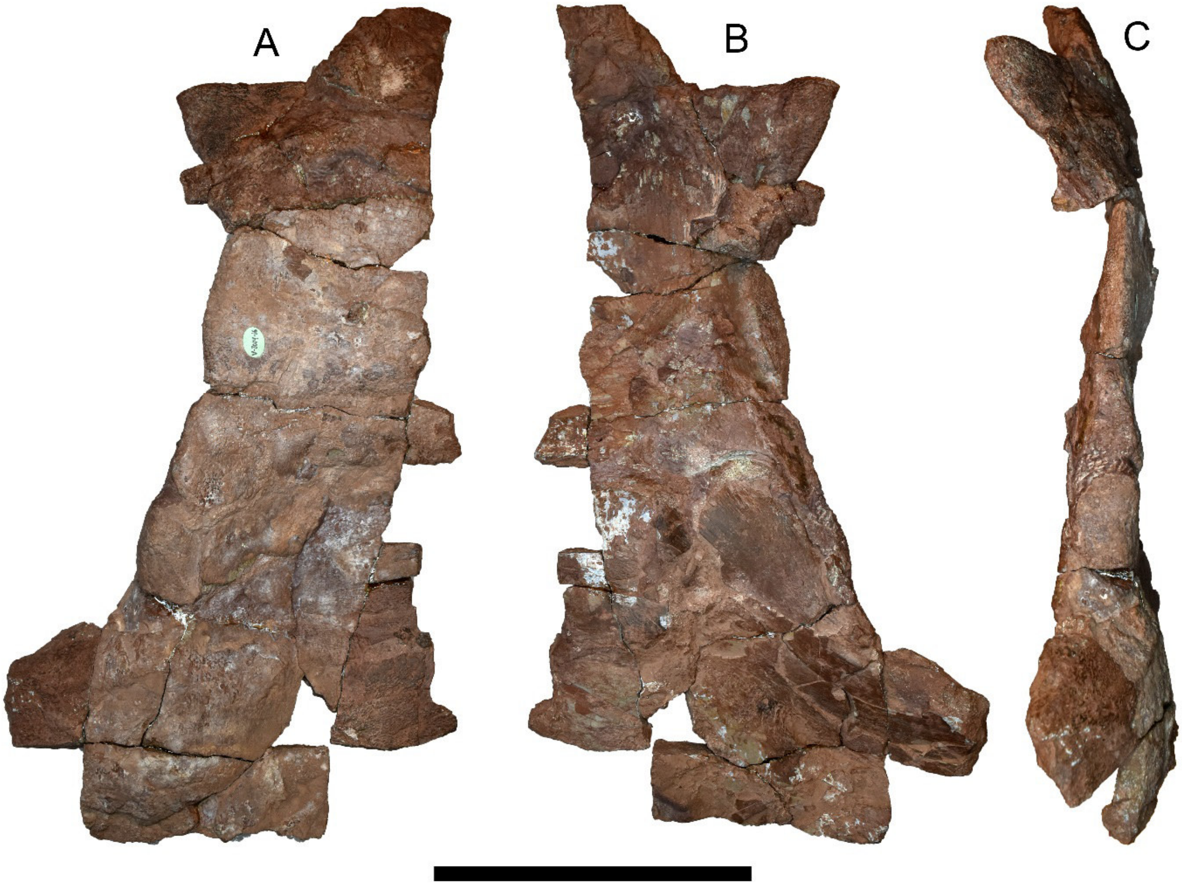

Figure 5.7 - NHMD Testudinata n. gen. et sp. holotype. Plastron element NHMD 163409 F and 163408 in A, dorsal; B, ventral; and C, lateral views. Scale bar equals 10 cm.

At least seven elements are associated to NHMD Testudinata n. gen. et sp. plastron. The most complete and diagnostic part is made of the two elements NHMD 163409 F and 163408, that together form the right anterior piece of the plastron, including part of the right epi-, ento-, hyo-, and mesoplastra (Fig. 5.7; S5.2–5.03). The entire piece is deformed dorsoventrally, being gently S-shaped in medial view. In ventral view, the plastron of NHMD Testudinata n. gen. et sp. is characterized by at least four gular and intergular spines, two right preserved in NHMD 163409 F and two left preserved in NHMD 163409 D (Fig. 5.8B). Only in the right part bone sutures and scute sulci are appreciable. The epiplastron of NHMD Testudinata n. gen. et sp. bears both extragular and gular spines. In ventral view, the lateralmost spine is completely covered by the gular, while the medial spine bears the sulcus between the extragular and gular scutes. This sulcus runs anteroperipherally and lateromedially until the contact with the humeral sulcus. The humeral sulcus runs anteromedially to posterioperipherally, almost parallel and slightly more anteriorly than the epiplastral suture. A small protuberance below the lateral protrudes dorsally as a strong tuberosity and may be identified as the dorsal process of the epiplastron. In the carapace the contact should be anterior to the scapula attachment, but NHMD Testudinata n. gen. et sp. there seems to be no fusion with the dorsal process of the epiplastron. In dorsal view, the base of the epiplastron shows the scar attachment for the cleithrum. The entoplastron of NHMD Testudinata n. gen. et sp. in

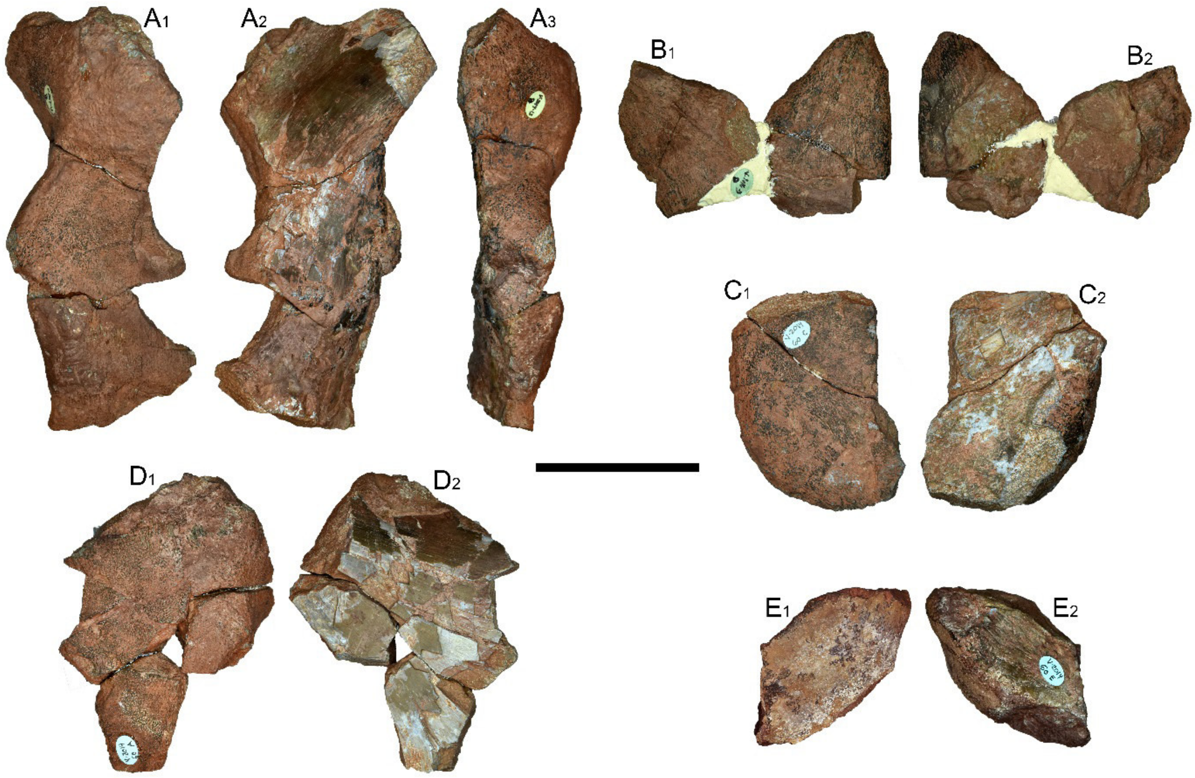

Figure 5.8 - NHMD Testudinata n. gen. et sp. holotype. Plastron elements. A, NHMD 163409 B; B, NHMD 163409 D; C, NHMD 163410 C; D, NHMD 163410 A; E, NHMD 163410 E. Subscripts: 1, dorsal view; 2, ventral view; 3, lateral. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

ventral view appears as a small, half rhombic element, more acute anteriorly. The suture with the epiplastron is faint and runs parallel to the anterior sulcus of the humeral scute, while the suture with the hypoplastron is enlightened by a small but step. Dorsally, the preserved part of the entoplastron bears no dorsal process. Ventrally, the hyoplastron of NHMD Testudinata n. gen. et sp. contacts anteriorly with both the epi- and entoplastra. The contact with the mesoplastron is posterior to the the axillary notch, runs anteromedially to posteroperipherall, and is appreciable also in dorsal view. The hyoplastron thickness close to the axillary notch is almost four times the medial thickness. The axillary notch is a gentle curvature forming an angle of about 130° with the lateral margin of the plastron. At almost half the length of the hypoplastron, the humeral and pectoral scutes form a sulcus running slightly inclined lateromedially. The pectoral scute covers entirely the axillary notch.

Elements NHMD 60 A and 163409 B come, respectively, from the right and the left abdominal-femoral area of the plastron (Fig. 5.8). They both bear part of the correspondent inguinal notch. 60A belongs entirely to the right hypoplastron, while 163409 B bears posteriorly a small fragment of we identify as the xiphiplastron. In ventral view, both 163409 B and 60 A show the femoral scute contacting with the abdominal scute anteriorly, with a sulcus running straight and medioperipherally into the inguinal notch (Fig. 5.8). The inguinal notch is better preserved in 163409 B. In ventral view, the inguinal notch is a steep, slightly inclined anteromedially concavity, with the anterior border projecting dorsoperipherally.

The anal area of NHMD Testudinata n. gen. et sp. plastron is represented by the right element 60 E and the left element 163409 C (Fig. 5.8). They both preserve the posteriormost curvature of the plastron and indicate that the xiphiplastra thickened posteriorly, as noticeable both in medial and peripheral view in 163409 C (Fig. 5.8C). The curvature of both elements is subrounded and, especially the straight, posterior border preserved in 163409 C, let us conclude that NHMD Testudinata n. gen. et sp. did not had an anal notch. No scute sulci are present, meaning that these two elements were entirely covered by the anal scute.

Shoulder Girdle

NHMD Testudinata n. gen. et sp. has both scapula-coracoids preserved. The left scapulacoracoid NHMD 163389 A (Fig. 5.9; S5.4) misses the acromion process of the scapula and part of the coracoid blade, while it preserves entirely the dorsal scapular process. The entire specimen seems slightly deformed lateromedially, and the scapulocoracoid suture was entirely reconstructed during the preparation. In the right scapulacoracoid NHMD 163390 A (Fig. 5.10; S5.5), the coracoid misses its

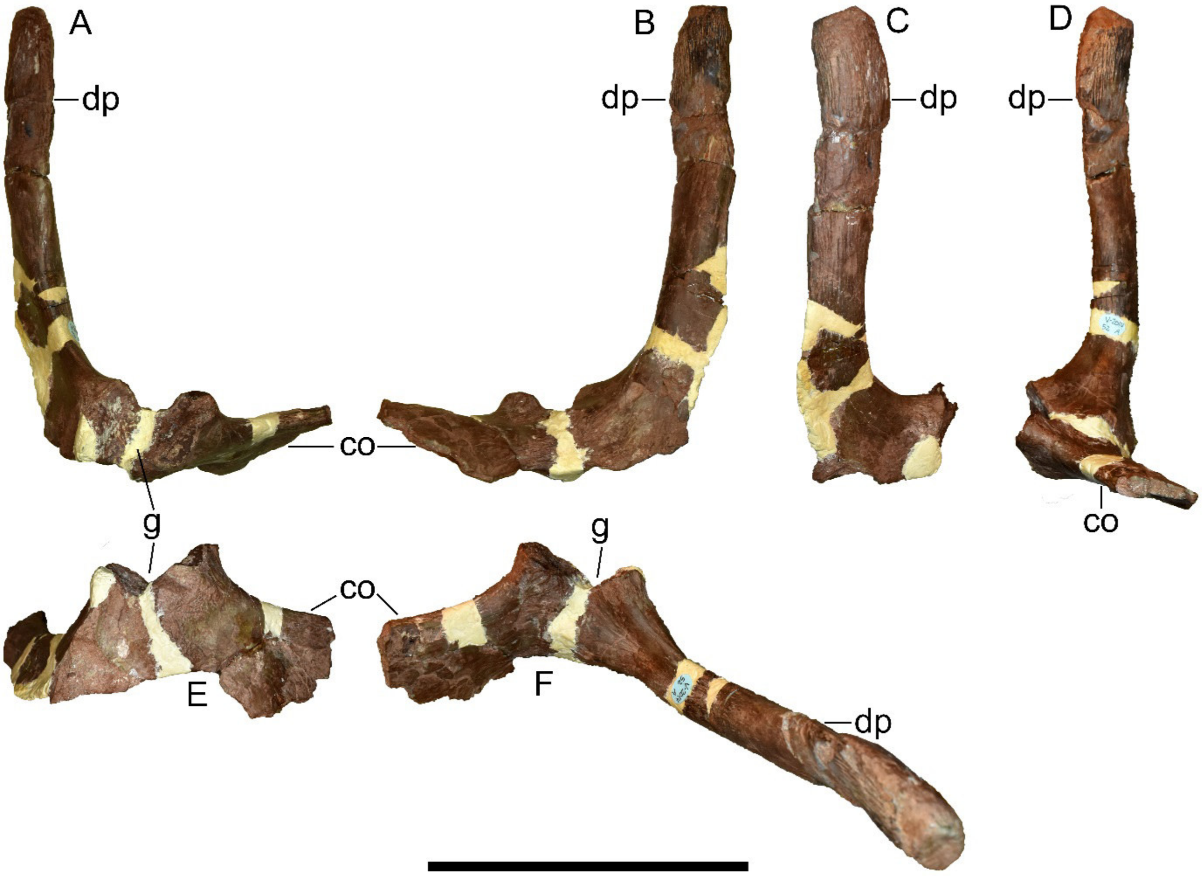

Figure 5.9 - NHMD Testudinata n. gen. et sp. holotype. Left scapulacoracoid NHMD 163389 in A, lateral; B, medial; C, anterior; D, posterior; E, ventral; and F, dorsal views. Abbreviations: **co**, coracoid; **dp**, dorsal process; **g**, glenoid. Light yellow parts were reconstructed during preparation. Scale bar equals 10 cm.

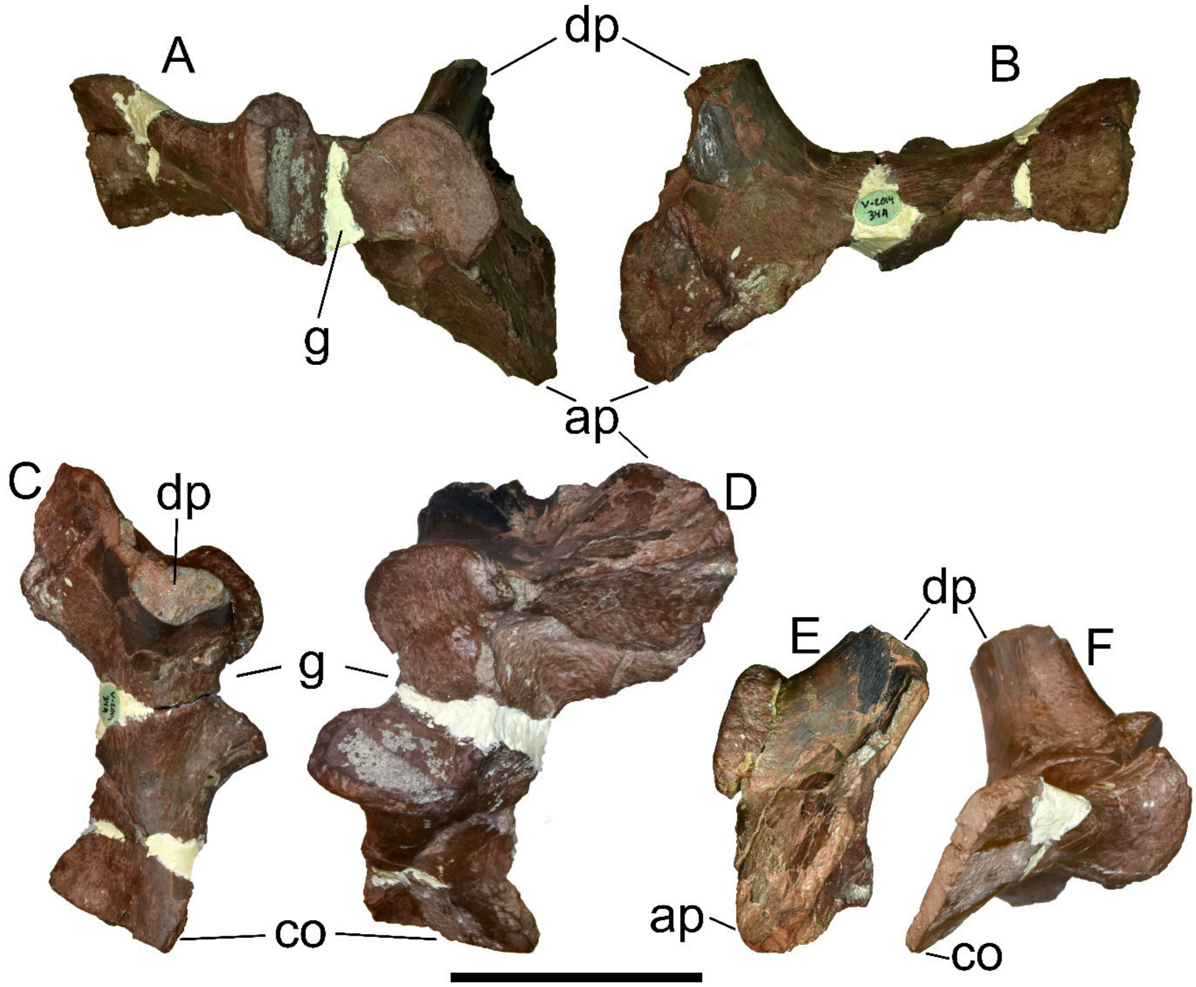

Figure 5.10 - NHMD Testudinata n. gen. et sp. holotype. Right scapulacoracoid NHMD 163390 in A, lateral; B, medial; C, dorsal; D, ventral; E, anterior; and F, posterior views. Abbreviations: **ap**, acromion process; **co**, coracoid; **dp**, dorsal process; **g**, glenoid. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

blade; the scapula preserves the acromion process and a small proximal portion of the distal process, while its distal end is preserved as the separate specimen NHMD 163390 B. The entire specimen seems less deformed than NHMD 163389 A.

In NHMD Testudinata n. gen. et sp., the scapula preserves its acromion process only in the right specimen NHMD 163390 A as a massive, pyramidal flange projecting ventroanteriorly. The acromion is defined by three flat and somewhat concave faces, project respectively anteromedially, anterolaterally, and posteriorly. The three ridges identified by the contact of these three facets are sharp and well defined. The anterior ridge is straight, while the two posterior ridges are convex and bear a strong prominence at about half of their length. The entire length of the acromion process is less than a third of the length of the scapular dorsal process. The scapular facet of the glenoid is a mostly flat, broad, subcircular surface, gently projecting anteriorly at its laterodistal margin. The dorsal process of the scapula is preserved entirely only in the left specimen 163389 A. It is a long, slender column triangular in proximal cross section and lenticular in distal cross section. It is almost perpendicular to the plane of the coracoid blade, forming an angle of about 85°. In lateral view, it gently bows anteriorly. The lateral ridge of the dorsal process is a sharp crest that runs from the acromion process proximally to the mid length of the dorsal process, turning to a smoother and gentler saddle-like crest in the distal half of the dorsal process. The distal third of the dorsal process presents a longitudinally organized rugosity, absent along the rest of the process and present both in the left and right specimens (like in *Proterochersis*).

In NHMD Testudinata n. gen. et sp., both shoulder girdles preserve partially the coracoids as glenoid facet, with both glenoid plates missing their distal part. The glenoid facet of the coracoid is concave and oval (with the major axis directed dorsoventrally), and slightly smaller than the scapular facet. The coracoid blade is flattened dorsoventrally, with the lateral margin thicker and more rounded than the posterior margin. Both specimens seem to be missing the coracoid foramen.

Forelimbs

NHMD Testudinata n. gen. et sp. has elements from both forelimbs. The humeri are preserved only as proximal ends both in the left element NHMD 163396 A and in the right one NHMD 163390 C (Figs. 5.11–5.12; S5.6). The head of the humerus and the two processes have a general rugose aspect, while the small preserved portion of the shaft is smooth. The head of the humerus is saddle-like shape on the glenoidal surface and projects more proximally than both the medial and the lateral processes. The humeral head projects dorsolaterally with a hook-shaped distal ridge that forms on the upper proximal part of the head and runs first laterally, then descending and curving posteriorly toward the medial axis of the head. The medial process projects proximally little lower the humeral head but higher than the lateral process; it is less prominent than the lateral process and is connected to the humeral head by a shallow concavity. In ventral view, below this concavity there is a wide subcircular depression, bordered on its upper lateral part by a ridge that runs from the bottom of the concavity to the half height of the

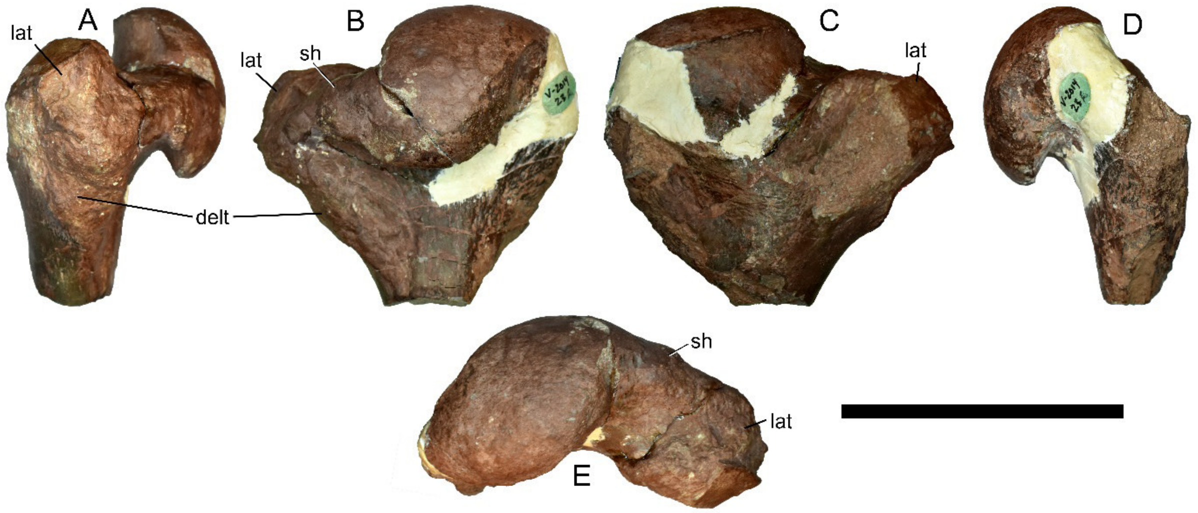

Figure 5.11 - NHMD Testudinata n. gen. et sp. holotype. Left humerus NHMD 163396 A in A, posterior; B, dorsal; C, ventral; D, anteriro; and E, proximal views. Abbreviations: **delt**, deltopectoral crest; **lat**, lateral process; **sh**, shoulder. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

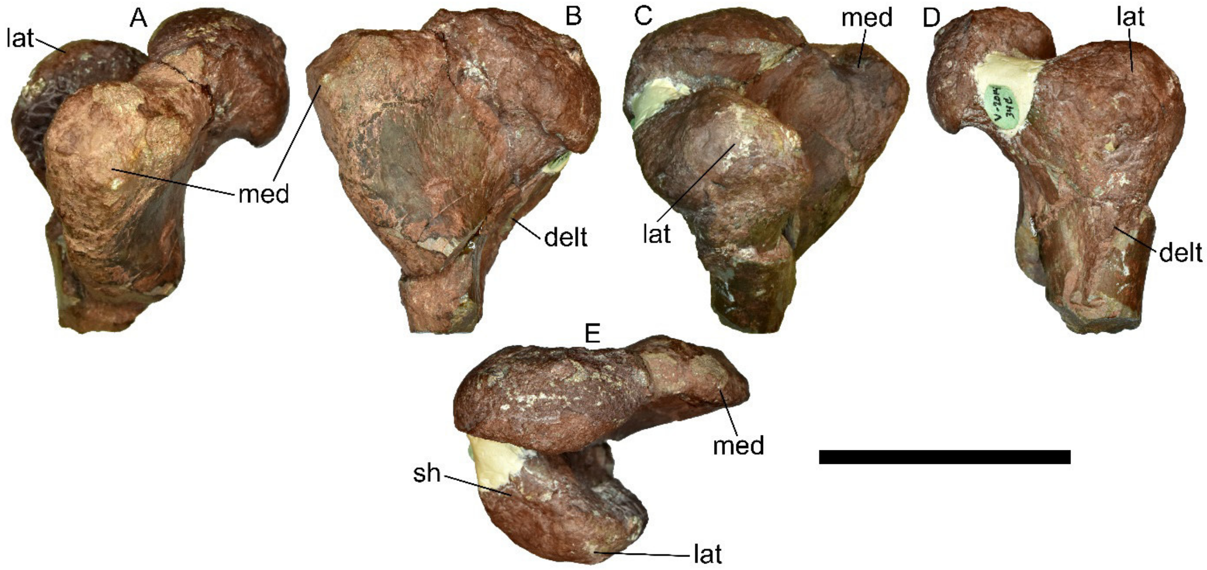

Figure 5.12 - NHMD Testudinata n. gen. et sp. holotype. Right humerus NHMD 163390 C in A, posterior; B, dorsal; C, ventral; D, anterior; and E, proximal views. Abbreviations: **delt**, deltopectoral crest; **lat**, lateral process; **med**, medial process; **sh**, shoulder. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

lateral process. The lateral process is sub-triangular in shape in proximal view; despite its attachment with the humeral head was reconstructed during preparation in the right humerus NHMD 163390 C, the presence of a shoulder seems unequivocable, as in cryptodiran turtles. The lateral process projects medially, somehow invaginating toward the middle line of the humerus, rather than projecting outward, and forming a V-shaped fossa with the medial process. The deltopectoral crest is lightly preserved on the anterior side of the lateral process as a ridge running medially from the anterior part of the humeral shaft to the ventrolateral base of the lateral process.

The left radius NHMD 163389 D misses the distal end (Fig. 5.13). The proximal end is complete and presents a head slightly rugose and triangular in proximal view. In lateral view, the head is concave for the contact with the humerus. Laterally, the articulation with the ulna is a small slightly concave and triangular surface bordered by two conspicuous longitudinal ridges, the left one running distally, the right one distolaterally. A third more conspicuous, long, and bulged ridge runs anterolaterally from the mid part of the anterior side of the head to a knob, corresponding to the process for the proximal radio-ulnar ligament. The proximal process for the radio-ulnar ligament is closer to the mid-section of the radius shaft, rather than proximally, closer to the head. The distal process of the radio-ulnar ligament is not preserved. The radius shaft is smooth and subcircular in mid-section, flattering dorsoventrally in the distal section, showing the beginning of the distal expansion.

The ulna consists of the left proximal half NHMD 163389 C (Fig. 5.14). In proximal view, the ulna has a somewhat deltoid shape, with the longer axis crossing lateromedially. The olecranon protrudes proximally from the lateral part of the ulna with a trapezoidal section at its base, and a pointed apex. The entire olecranon is so delimited by four surfaces: a flat surface facing medially into the

Figure 5.13 - NHMD Testudinata n. gen. et sp. holotype. Left radius NHMD 163389 D in A, lateral; B, ventral; C, dorsal; D, medial; and E, proximal views. Abbreviations: **rua**, radio-ulnar articulation; **rul**, radio-ulnar ligament. Scale bar equals 5 cm.

sigmoid notch, another flat surface facing ventrally, one concave surface facing dorsolaterally, and one smaller surface, slightly convex, facing laterally. The latter two surfaces are separated by a longitudinal, shallow crest running distally from the apex of the olecranon, until reaching the lateral, sharp edge of the ulnar shaft. In ventral view, the sigmoid notch has a gentle concavity with an angle of over 120° and there is no evidence of the sigmoid ridge on the proximal articular surface. From the medioventral margin of the sigmoid notch a prominent knob projects mediolaterally. Another prominent structure projects from the mediodorsal margin of the sigmoid notch, first as a proximal notch, then turning to a ridge that runs dorsomedially until the attachment of the bicipital tendon. The bicipital tendon

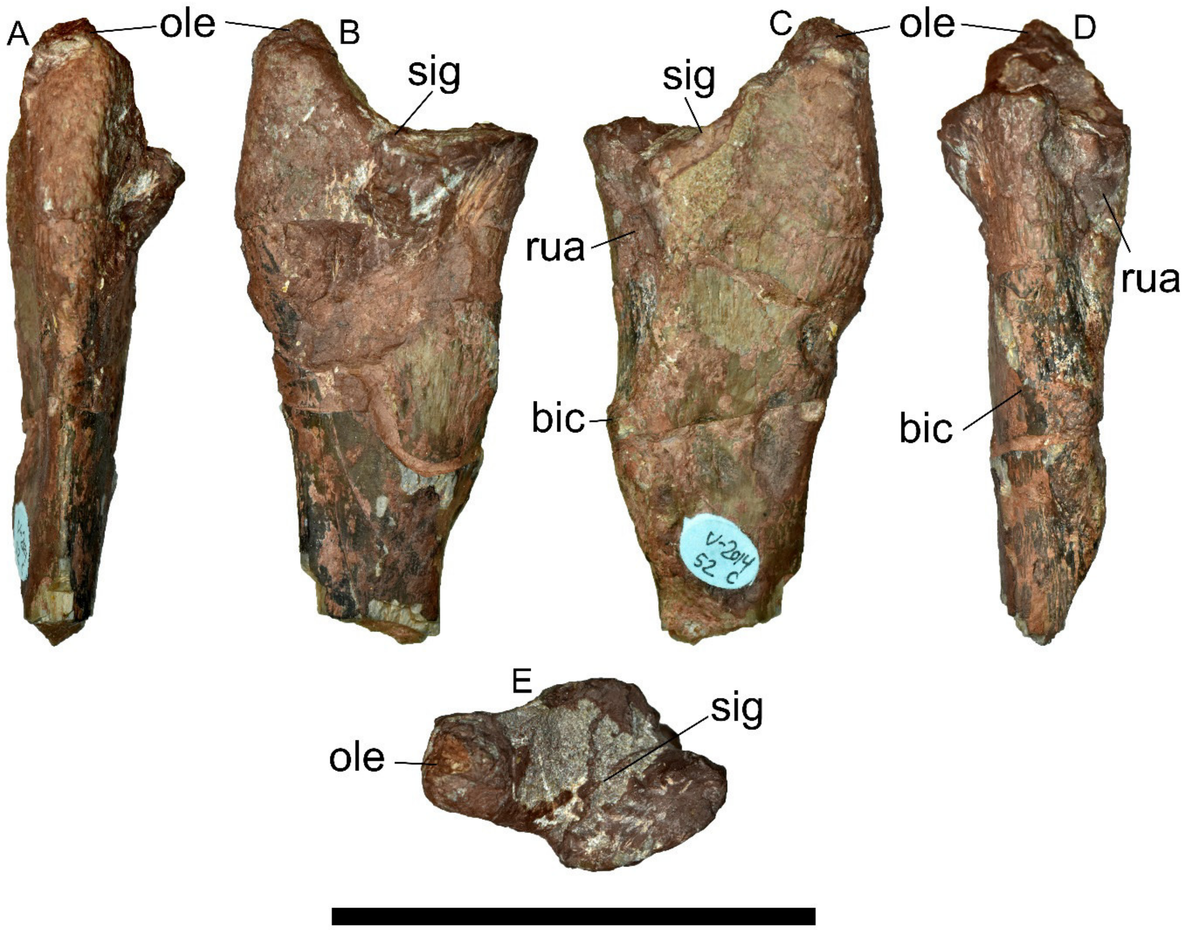

Figure 5.14 - NHMD Testudinata n. gen. et sp. holotype. Left ulna NHMD 163389 C in A, posterior; B, dorsal; C, ventral; D, anteriro; and E, proximal views. Abbreviations: **bic**, bicipital tendon attachment; **ole**, olecranon; **rua**, radio-ulnar articulation; **sig**, sigmoid notch. Scale bar equals 5 cm.

attachment is a strong, oval tubercle that characterizes the medial side of the ulnar shaft. The abovementioned ridge-like structure, the bicipital tendon attachment tubercle, and the medioventral margin of the ulnar shaft identify a wide, sub-triangular, concave surface for the articulation of the radius. The ulnar shaft is triangular in section and tapers toward the midsection. The ulnar shaft is characterized by a lateral sharp edge and a medial flat surface.

Pelvic girdle

NHMD Testudinata n. gen. et sp. has both sides of the pelvic girdle preserved. NHMD 163406 is the right pelvis with complete acetabulum and ilium, and partial pubis and ischium (Fig. 5.15; S5.07). NHMD 163396 B is the left pelvis, which preserves entirely the acetabulum and part of the ilium, the pubis, and the ischium (Fig. 5.16). Element NHMD 163406 is also the best preserved of the two elements, where 23 B seems to have been somehow deformed mediolaterally and dorsoventrally.

In NHMD Testudinata n. gen. et sp. , the acetabulum is sub-triangular in shape, with the upper angle projecting posteriorly and laterally. The three pelvic elements are fused. The ilium contributes for

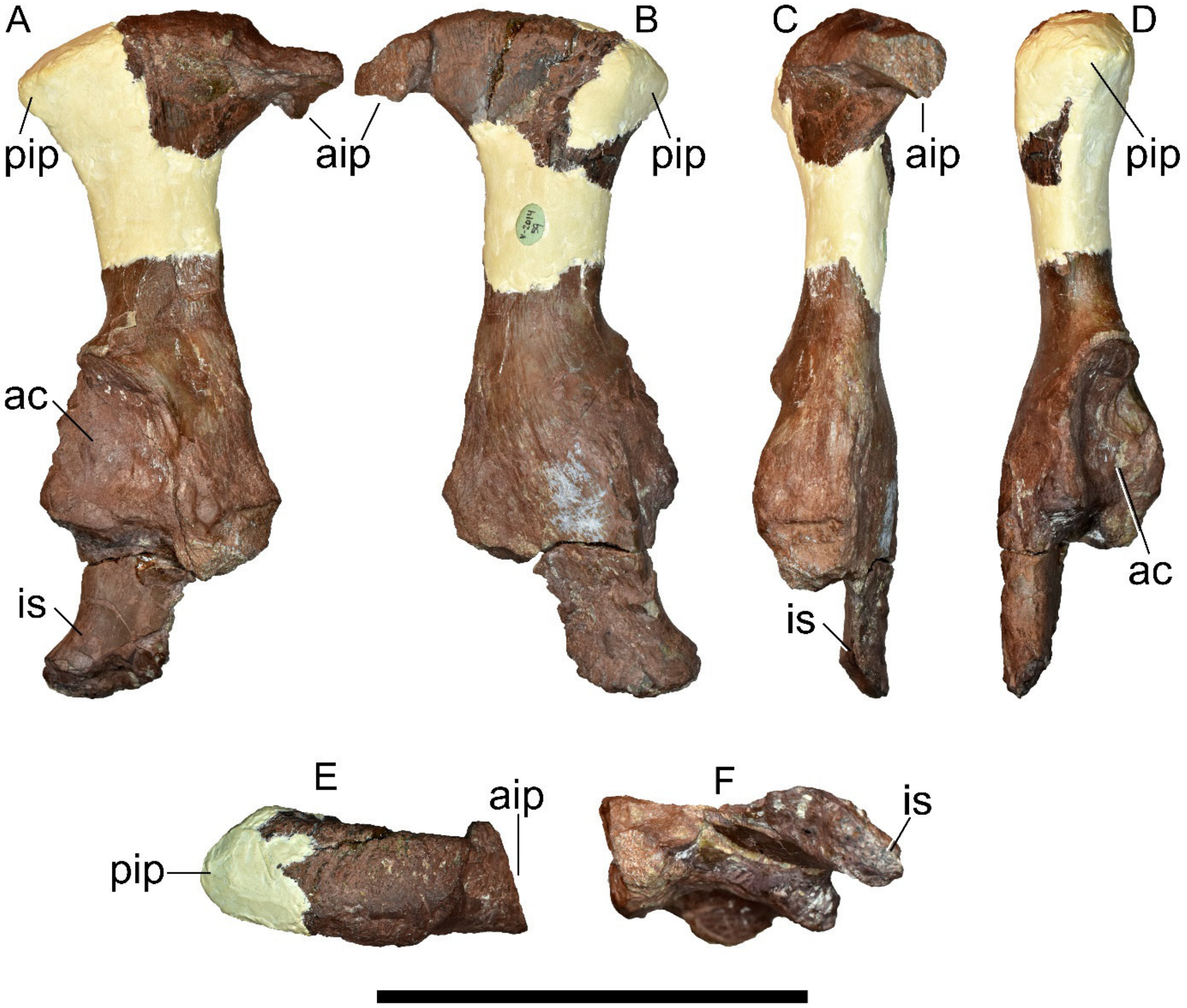

Figure 5.15 - NHMD Testudinata n. gen. et sp. holotype. Right pelvis NHMD 163406 in A, lateral; B, medial; C, anterior; D, posterior; E, dorsal, and F, ventral views. Abbreviations: **ac**, acetabulum; **aip**, anterior ilial process; **is**, ischium; **pip**, posterior ilial process. Light yellow parts were reconstructed during preparation. Scale bar equals 10 cm.

the most to the acetabulum, followed by the ischium, and the pubis. The margin running from the ischium to the pubis is a thick ridge with a concavity at its middle length; the acetabular facet presents two small but deep and lenticular depressions at this concavity, with a dorsoventral elongation.

The ilium is complete in the right element NHMD 163406. The ilium neck is an elongated, dorsal protrusion, lenticular in section. The most of it has been reconstructed during preparation, and so has been part of the posterior ilial process. The ilial distal end is an anteroposterior expansion, with a dorsal, saddle-like surface that protrudes posteriorly, forming the posterior ilial process, and anteriorly, forming the anterior ilial process. The anterior process of the right ilium preserves a fractured surface that, together with the dorsal surface of the neck, may corresponds to the bone suture between the ilium and the carapace. In lateral view, the curvature of the posterior process is gentler and less arcuate than that of the the anterior process.

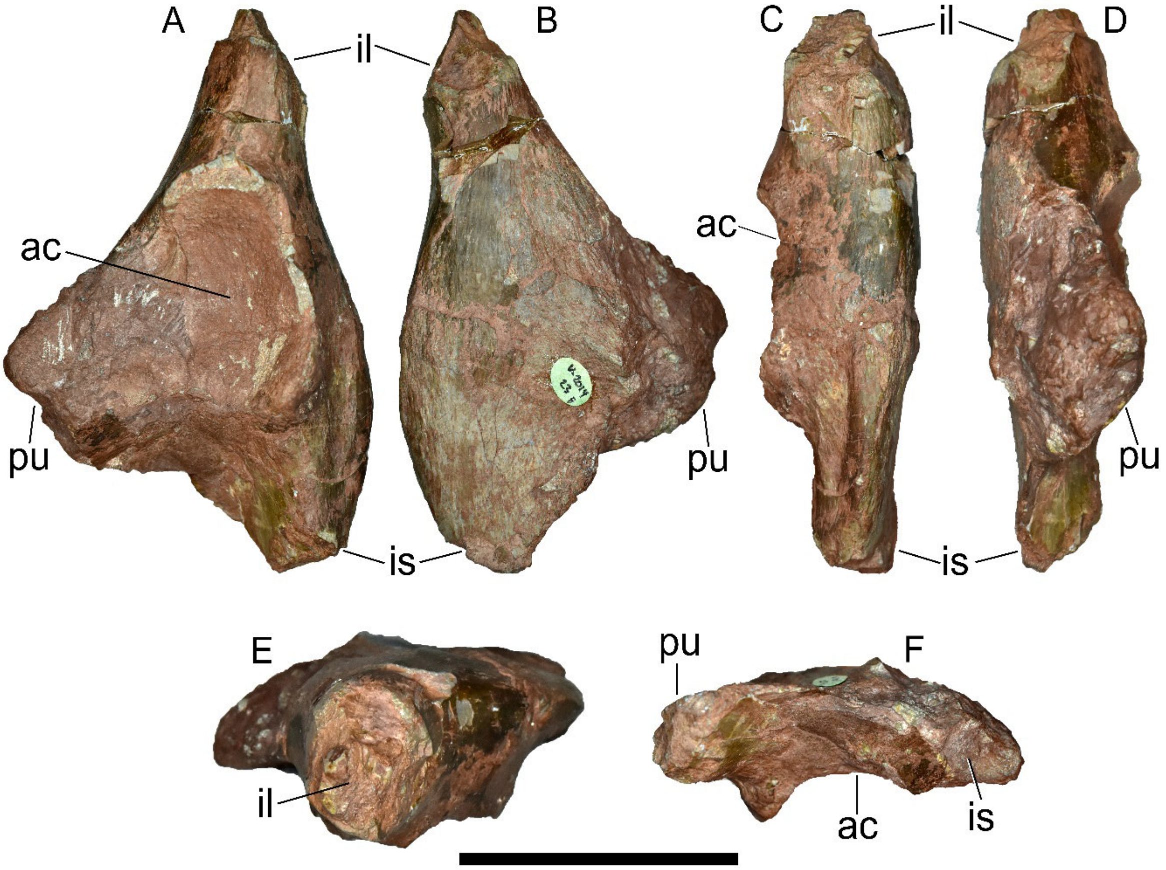

Figure 5.16 - NHMD Testudinata n. gen. et sp. holotype. Left pelvis NHMD 163396 B in A, lateral; B, medial; C, posterior; D, anterior; E, dorsal, and F, ventral views. Abbreviations: **ac**, acetabulum; **il**, ilium; **is**, ischium; **pu**, pubis. Scale bar equals 10 cm.

The pubis and the ischium are partially preserved and mostly in their acetabular part. The anterior margin of the ilial neck runs ventrally forming the medial margin of the pubis, which has a thick, compact aspect in anterior view. The ischium presents a small portion of the ischial lateral process, which runs posterolaterally. In posterior view, the ischial lateral process forms a conspicuous ridge that runs ventrally.

Hindlimbs

Elements from both hindlimbs are preserved in NHMD Testudinata n. gen. et sp. NHMD 163398 A-B represent the distal and the proximal halves of a right femur (Fig. 5.17; S5.8–5.9), with only a small portion of the midshaft and the tibial condyle missing, while NHMD 163389 B and NHMD 163396 D are, respectively, the proximal and distal end of a left femur (Fig. 5.18). In acetabular view, the femoral head outline is lenticular, being almost twice tall than wide. The main axis of the femoral head is diagonally inclined with respect to the femoral body. The femoral head is slightly more proximal positioned than the trochanter major, and both bridged by a bone lamina that constricts anteroposteriorly and that is slightly concave proximally. The femoral head is considerably offset in respect to the femoral shaft, rather than being anteriorly positioned. The ventromedial corner of the femoral head projects

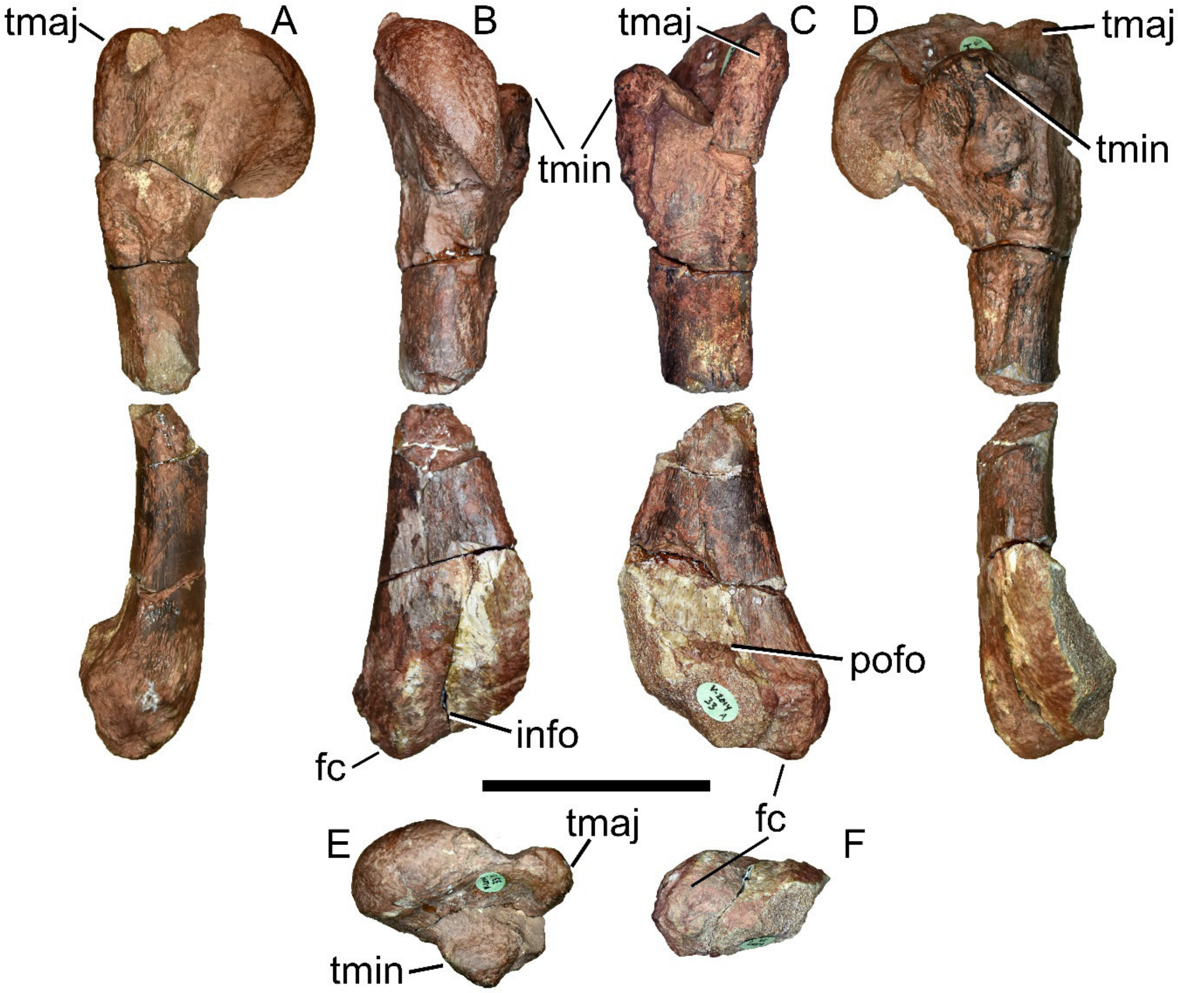

Figure 5.17 - NHMD Testudinata n. gen. et sp. holotype. Right femur NHMD 163398 A-B in A, posterior; B, dorsal; C, ventral; D, anterior; E, proximal, and F, distal views. Abbreviations: **fc**, fibular crest; **info**, intercondylar fossa; **pofo**, popliteal fossa; **tmaj**, trochanter major; **tmin**, trochanter minor. Light yellow parts were reconstructed during preparation. Scale bar equals 5 cm.

distally, forming a notch with the femoral shaft. Between the femoral head condyle and the anterior facet of the femur, there is a conspicuous ridge that curves from the top of the femoral head to the ventromedial corner of the femoral head. The anterior facet of the femur presents two prominent rugose tuberosity: a more central one, for the insertion of the puboischiofemoralis internus, and a more lateral one, insertion for the ischiotrochantericus. The trochanter major is on the same alignment than the main axis of the femoral head. The trochanter major is slightly curved anteriorly, forming with the trochanter minor a V-shaped angle of about 50° in the intertrochanteric fossa. There is no bridge between the two trochanters. The proximal end of the trochanter minor is at the same level of the mid height of the femoral head. The thickness of the trochanter minor pillar is nearly double than the pillar of the trochanter major. To the posterior facet of the trochanter minor, there are conspicuous tuberal rugosities for muscle attachment. The connection between the femoral head and the trochanter minor is excavated by a saddle-like bridge that forms a proximal notch. The midshaft is round in section, slightly flatter on

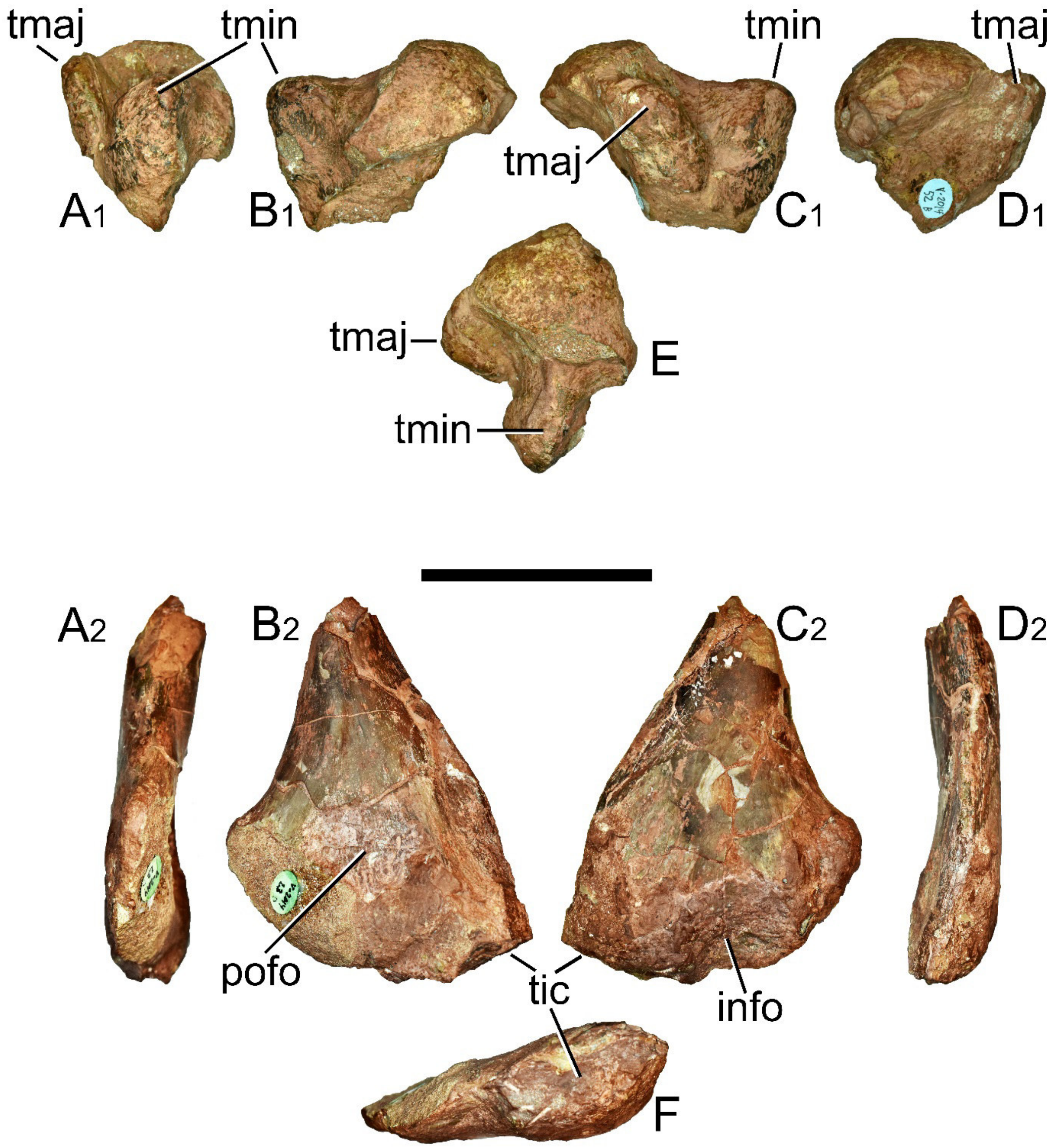

Figure 5.18 - NHMD Testudinata n. gen. et sp. holotype. Left femur NHMD 163389 B (up) and 163396 D (bottom) in A, anterior; B, dorsal; C, ventral; D, posterior; E, proximal, and F, distal views. Subscripts: 1, proximal; 2, distal. Abbreviations: **info**, intercondylar fossa; **pofo**, popliteal fossa; **tic**, tibial condyle; **tmaj**, trochanter major; **tmin**, trochanter minor. Scale bar equals 5 cm.

its lateral side, and producing a subtle D-shaped outline in cross section. The narrowest part of the femur is at midshaft, extending distally. The femoral body forms a laterally concave gentle arch. The tibial condylar groove is subrounded, forming a prominent ridge ventrally. The intercondylar fossa is appreciable dorsally, while the popliteal fossa is slightly appreciable ventrally in NHMD 163398 A, due to the lack of the tibial condyle and a longitudinal wide fracture. NHMD 163396 D has a tibial condyle projecting more proximally than the fibular condyle. The tibial condyle is fractured ventrolaterally.

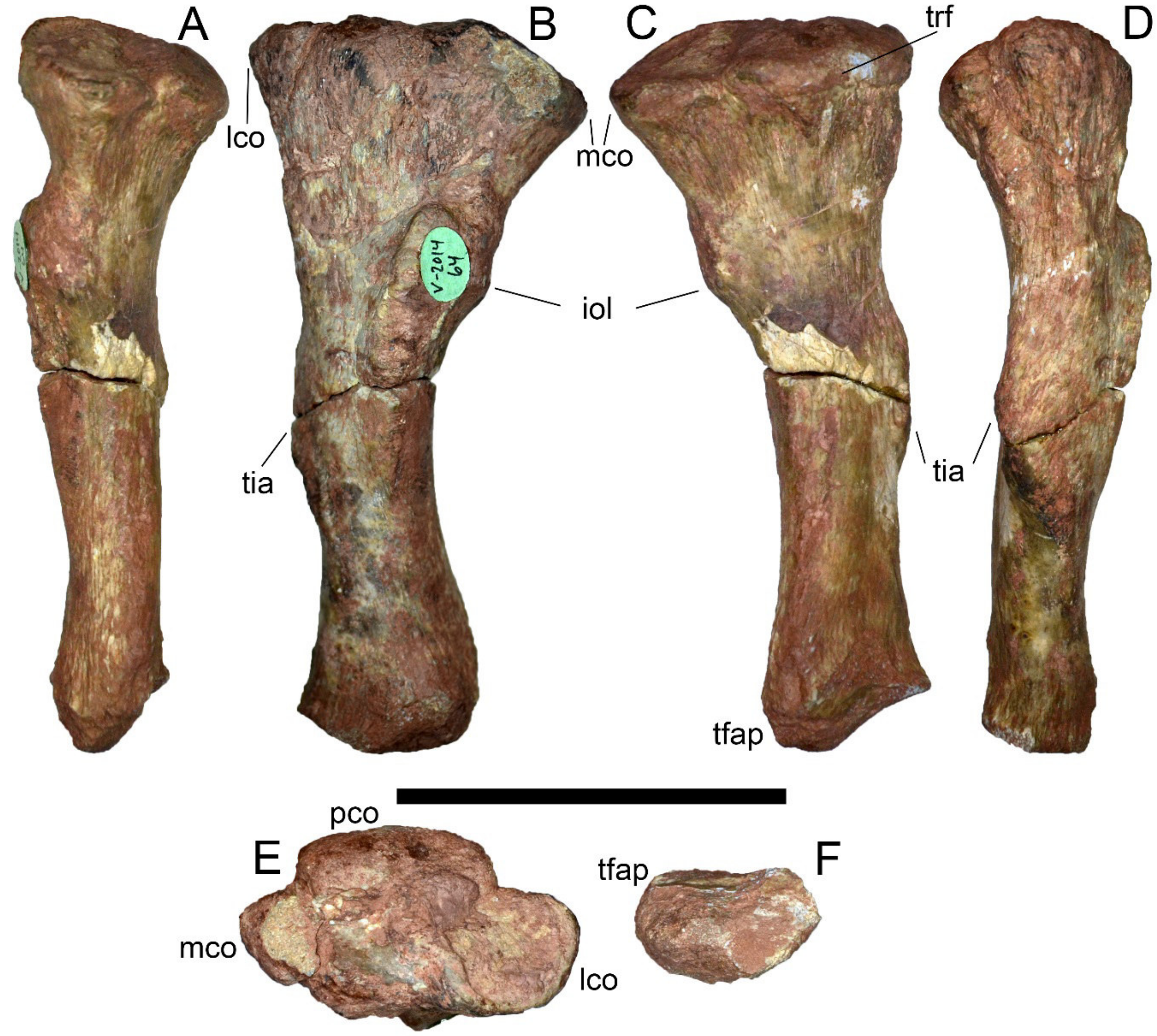

Figure 5.19 - NHMD Testudinata n. gen. et sp. holotype. Right tibia NHMD 163393 in A, medial; B, dorsal; C, ventral; D, lateral; E, proximal, and F, distal views. Abbreviations: **iol**, interosseous ligament; **lco**, lateral condyle; **mco**, medial condyle; **pco**, posterior condyle; **tfap**, tibial facet for the ascending process of astragalus; **tia**, tibialis anterior; **trf**, triceps femoris. Scale bar equals 5 cm.

Dorsally, the two condyles are separated by a shallow intercondylar fossa. Ventrally, the popliteal fossa forms a wide, rugose, subcircular depression right above the tibial articular surface and does not reach the edge of the articulation but is instead surrounded distally by a ridge running between the two condyles.

The right tibia NHMD 163393 is the best preserved (Fig. 5.19; S.10), while NHMD 163395 A is the proximal end of the left tibia (Fig. 5.20). The general aspect NHMD Testudinata n. gen. et sp. tibia is a stout, thick, long bone, with its proximal head almost thrice as wide as the narrowest point of the shaft. The head presents three major structures: a small lateral condyle, a stronger, subrounded medial condyle, and an oval posterior condyle. There is almost no distinction in the anterior contact of the medial and lateral condyles, while posteriorly both are separated from the posterior condyle by two small invaginations. The tibial proximal articular surface is divided in two anterior concave regions,

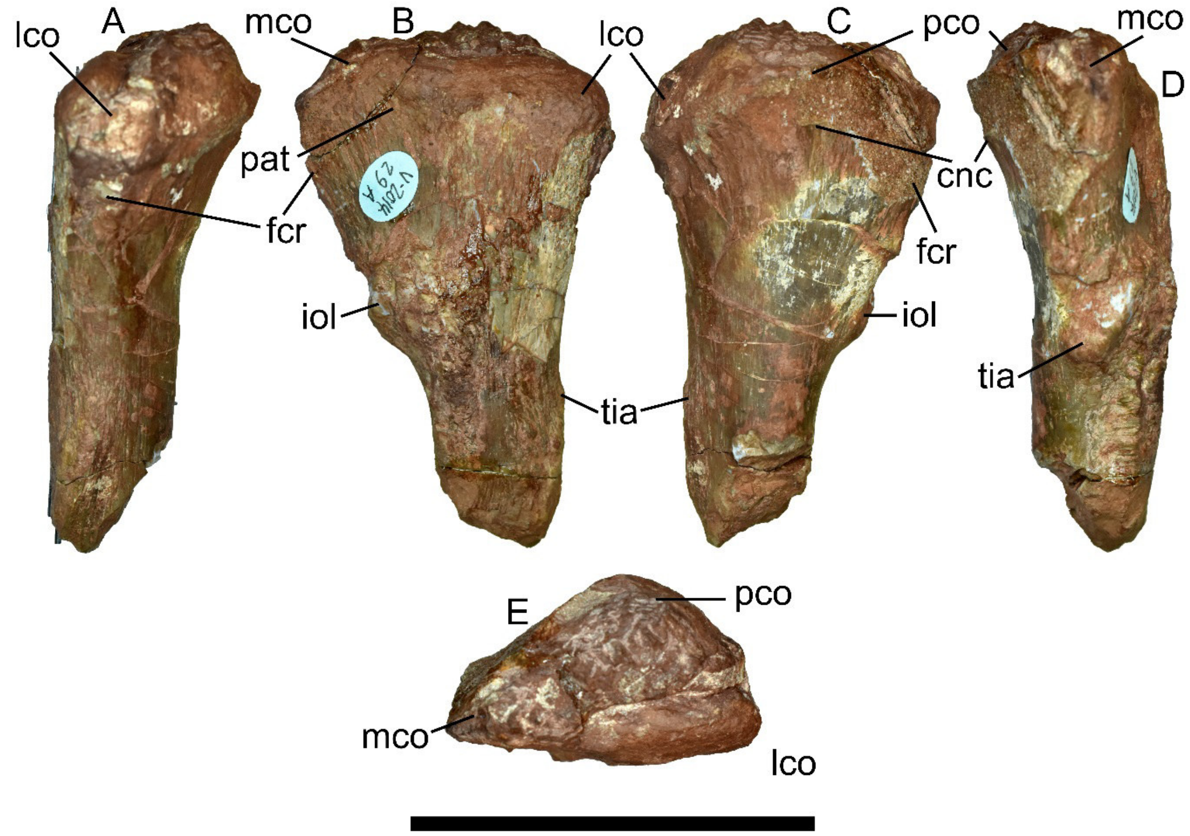

Figure 5.20 - NHMD Testudinata n. gen. et sp. holotype. Left tibia NHMD 163395 A in A, medial; B, dorsal; C, ventral; D, lateral; and E, proximal views. Abbreviations: **cnc**, cnemial crest; **fcr**, fibular crest; **iol**, interosseous ligament; **lco**, lateral condyle; **mco**, medial condyle; **pat**, patellar tendon attachment; **pco**, posterior condyle; **tia**, tibialis anterior. Scale bar equals 5 cm.

corresponding to the proximal surfaces of the lateral and medial condyles. These two concavities are divided by a sigmoidal crest that runs from the anterolateral margin of the medial condyle to the posterolateral margin of the lateral condyle. The proximal surface of the posterior condyle is smooth and convex. On its posterior margin, the contact between the upper smooth surface and a lower rugose area forms the crest for the attachment of the triceps femoris. The lateral condyle is a small, bulbous prominence that develops distally in a strong crest. Below the invagination between the lateral and the posterior condyle, a prominent tuberosity is evident. The medial condyle is bordered by a thick cnemial crest that runs distally until about a third of the entire tibial length. The cnemial crest contacts anteriorly with a prominent, heavy ridge that characterizes the entire anterior upper part of the tibial shaft. This strong ridge bows laterally and makes a proximal loop, possibly representing the attaching area for muscles and tendons. The tibial shaft strongly bows laterally, toward the fibula. A conspicuous groove, corresponding to the tibialis anterior attachment, is noticeable in the middle part of the tibial shaft. At the distal end of this groove, the tibial shaft reaches its narrowest diameter. The distal articular surface projects medially and is oval, with the major axis directed lateromedially. In ventral view, the lateral half is concave for the articulation with the calcaneus, while the medial half is a prominent knob, defined anteriorly by the tibial facet for the ascending process of the astragalus.

Phylogenetic Results

The phylogenetic analysis led to 16 most parsimonious trees, with a length (TL) of 1207 steps, consistency index (CI) of 0.269, retention index (RI) of 0.586 and a rescaled consistency index (RCI) of 0.158. A consensus tree is shown in Fig. 5.21, where NHMD Testudinata n. gen. et sp. has been recovered as sister taxon of the Late Triassic *Proganochelys* from Central Europe.

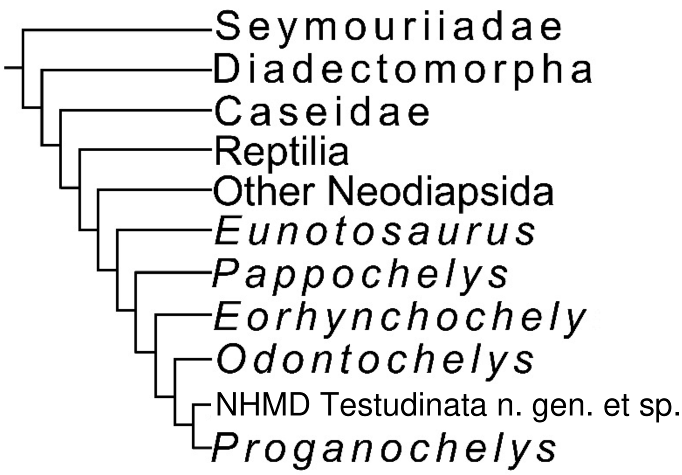

Figure 5.21 - Strict consensus tree of sixsteen MPTs of the phylogenetical matrix after Li et al. (2016) produced by a TNT 1.5 analysis (53 taxa, 280 characters: TL is 1207; CI is 0.269; RI is 0.586; RC is 0.158)

Comparison between NHMD Testudinata n. gen. et sp. and *Proganochelys*

The closest relative to NHMD Testudinata n. gen. et sp. is the Norian (Late Triassic) *Proganochelys*, known with three different taxa from Germany, Thailand, and New Mexico (USA). There are two main differences in the skeleton of NHMD Testudinata n. gen. et sp. and *Proganochelys*: (i) the iliac blade of NHMD Testudinata n. gen. et sp. expands anteriorly (ch. 213-1), contrary to *Proganochelys* (213-0); (ii) the arrangement of dorsal ribs in *Proganochelys* is fan shaped, with the distal ends of the ribs spanning further away than the proximal ends (ch. 259-1), while NHMD Testudinata n. gen. et sp. , though not presenting a complete carapace, seems to have dorsal ribs more or less parallel to one another.

Although not many differences are enlightened between the two taxa, we noticed at least seven autapomorphies for NHMD Testudinata n. gen. et sp. one of which is in the scapular girdle, where (I) the scapulacoracoid misses the coracoid foramen. Three autapomorphies are noticeable in the ulna, where (II) the proximal radio-ulnar ligament process weakly projects medially, (III) the radio-ulnar articulation is strongly concave, and (IV) the ulna does not present an evident sigmoid crest. Three other autapomorphie are visible in the hindlimbs, namely one in the femur, where (V) a subcircular popliteal fossa does not reach the edge of the condylar articulation and is distally surrounded by a ridge, and two in the tibia, characterized be (VI) a tibial proximal articular facet with two concavities separated by a crest and (VII) a tibial shaft that bears a dorsal massive ridge. A dubious potential autapomorphie of NHMD Testudinata n. gen. et sp. is the lateral process of the humerus projecting medially which, however, we cannot entirely confirm due to the fractured and partially preserved status of the left humerus and the uncertain reconstruction of the right one.

Figure 5.22 - Reconstruction of the Late Triassic Greenland Testudinata NHMD 190349. Carapace and caudal vertebrae in A, ventral and B, dorsal views. Scale bar equals 20 cm.

Preliminary considerations on two other Late Triassic Testudinata from Greenaland

At least two more specimens of Late Triassic Testudinata have been reported from Greenland (see Marzola et al. 2018). One of them, NHMD 190349 has been found during the Harvard-Denmark expedition of 1988 (A5) and is up-to-date in exhibition at the GeoCenter Møns Klint (Figs. 5.22–5.23; S5.10–5.18). It has briefly reported in Jenkins et al. 1994 as cf. *Proganochelys*, though this classification was based on two autapomorphies for this taxon that are not valid anymore.

A second specimen, NHMD 74737, has been recovered during the expedition in 2012 (Figs. 5.24–5.25; S5.19–5.25). Although its fragmentary condition and poor overall preservation, it presents a unique imbrication of the carapace scutes that seems unique among Testudinata (Figs. 5.24–5.25). Moreover, three vertebrae are associated to this specimen (S5.19–5.20). One isolated vertebra (possibly C4; S5.19) of 11 mm centrum length which is shorter posteriorly, and two articulated vertebrae (possibly C7 and C8; S5.20) more posterior 16mm long each. The total height of each vertebra is longer than the anteroposterior length of the centrum. The centrum is strongly amphicoelous, excavated laterally, which gives an hourglass outline in ventral view. The ventralmost margin bears a midline keel that forms an acute ventral margin. The ventral keel is also equally prominent along the centrum length and the ventral edge forms a straight line in lateral view. In axial view, the centrum is as wide as tall, but significantly longer than tall. The neural arch is taller than the centrum. The shape of C4 neural canal shows that this vertebra is slightly plastically compressed latero-dorsally. The transverse processes are positioned laterally between the dorsal part of the centrum and the pedestal. The transverse process projects latero-ventrally with no significant anterior or posterior projections. The pedestals are tall and represent more

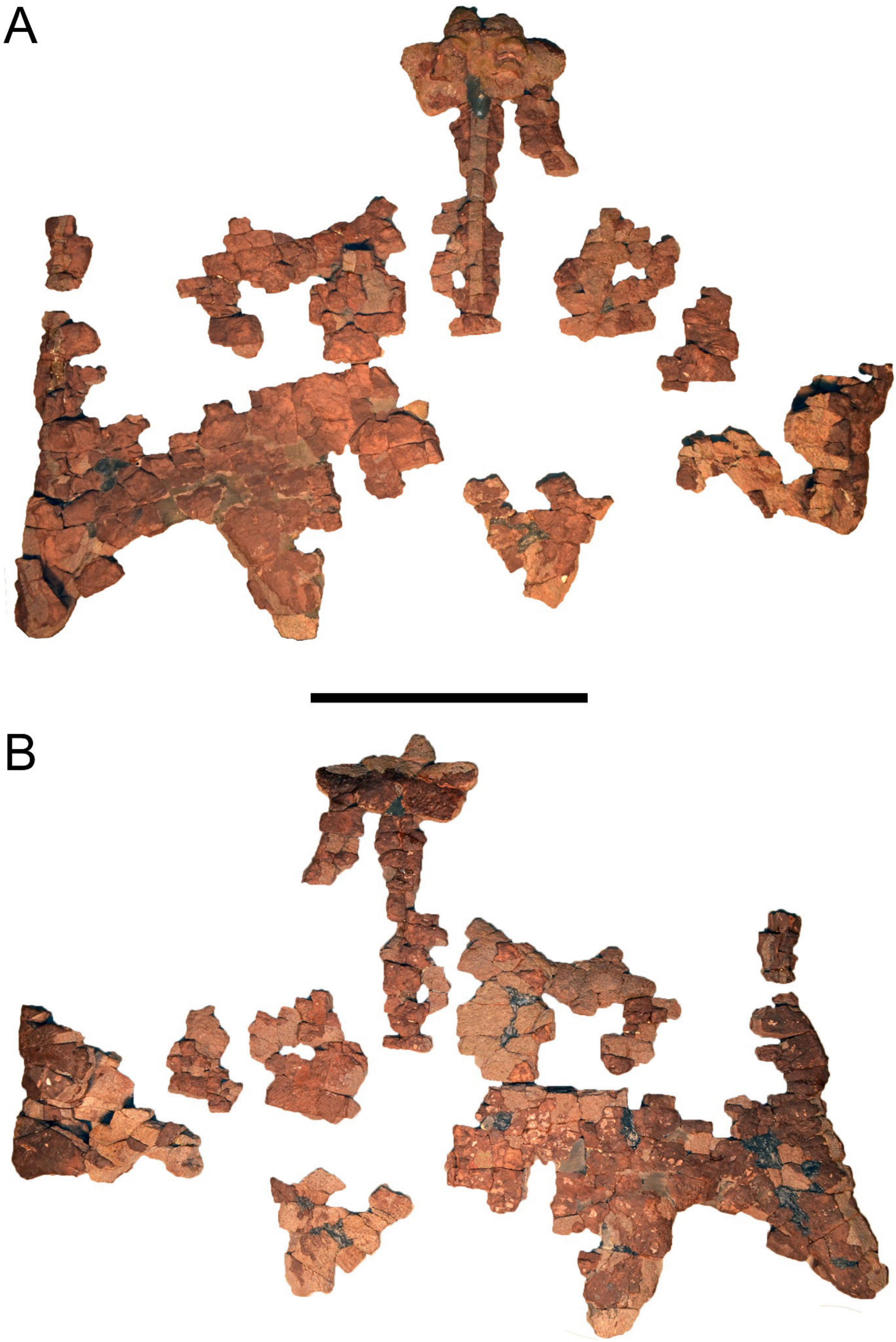

Figure 5.23 - Reconstruction of the Late Triassic Greenland Testudinata NHMD 190349. Plastron in A, dorsal and B, ventral views. Scale bar equals 20 cm.

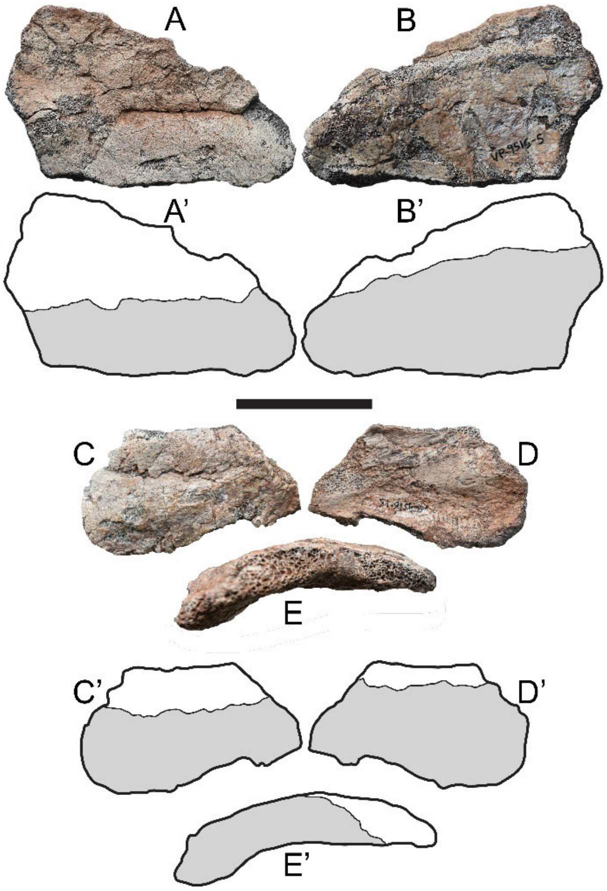

Figure 5.24 - The Late Triassic Greenland Testudinata NHMD 74737. Imbricated carapace scutes in A and C, dorsal; B and D, ventral; and E, lateral right views. A'–E' are interpretative drawings of A–E. Scutes in grey are posterior to the ones in white. Scale bar equals 5 cm; E and E' are enlarged x2.

than half of the height of the neural arch, making the neural canal taller than wide. The zygapophyses extend for 21 mm, ending both beyond and ahead of the centrum margins. Laterally, the prezygapophyses do not extend over the centrum lateral margins, in contrast to the postzygapophyses. The postzygapophyses are united in midline by a ridge. The neural spine is short (less than 2 mm tall) and about 5 mm long, thus representing only a small midline crest. The transverse processes are located close to the middle of the centrum and the right one is shorter than the left one. The ends of the transverse processes are oval, suggesting the contact for cervical ribs that, however, are not preserved. The articulation of the zygapophyses between C7 and C8 is concave in the prezygapophyses, making an articulation 7)8 (sensu Walther 1922; see also Joyce 2007). The prezygapophyses facets are verticalized, forming an acute angle between them.

Both these specimens are yet under study and their complete anatomical description and phylogenetic position is part of future developments.

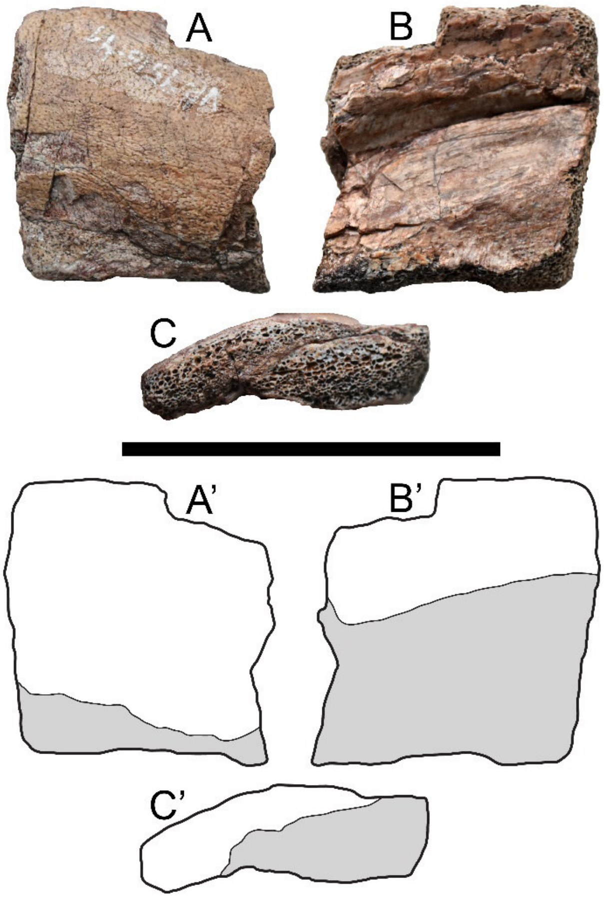

Figure 5.25 - The Late Triassic Greenland Testudinata NHMD 74737. An imbricated carapace scute in A, dorsal; B, ventral; and C, lateral left views. A'–C' are interpretative drawings of A–C. Scutes in grey are posterior to the ones in white. Scale bar equals 5 cm.

CHAPTER 6 – ANATOMICAL INSIGHTS OF THE FIRST LATE TRIASSIC THEROPOD OF GREENLAND

Abstract

NHMD Theropoda n. gen. et sp. n. gen. et. sp. is the first undoubtedly Late Triassic theropod dinosaur from Greenland. It is described on bone remains, that include a well-preserved pelvis and the pubis with one foramen only, scapular, and limb bones. The new taxon is a basal theropod and the best potential trackmaker for the innumerous tracks known in the area. The Late Triassic of Jameson Land Basin, east Greenland, reports a contrasting between the rarity of theropod bones and the abundance of theropod tracks; this is even more bizarre when compared to the rest of dinosaur and reptilian fauna, where bones are found more frequent than relative tracks. Such situation suggests that theropods were much more active and mobile in track-producing sediments. This high-activity might have resulted in an evolutionary advantage that leveraged theropods for being one of the most successful groups of reptiles.

Introduction

The presence of theropod dinosaurs patrolling the lacustrine environment of the Late Triassic Jameson Land (East Greenland) has been reported by innumerous tracks and trackways since the early 1980’s (Fig. 1).

Methods and Materials

The studied material is deposited at the Natural History Museum of Denmark (Copenhagen) as NHMD 74732, an articulated and fused left pelvis (ilium, pubis and ischium) only missing both pubic and ischial distal end, and a portion of the iliac anterodorsal margin (holotype) (Fig. 6.2); NHMD 195727, a left scapula; NHMD 195728, a right femur; NHMD 195729, a right femur R; NHMD 195730, a left femur; NHMD 195732, a skull fragment; NHMD 195733, a phalanx; NHMD 195734, a right scapula (Figs. 6.3–6.9).

Two expeditions to Jameson Land (East Greenland) were conducted by the GeoCenter Møns Klint and the Department of Geosciences and Natural Resource Management, Denmark in the Summers of 2012 and 2016 (Clemmensen et al. 216; Mateus et al. 2016; Marzola et al. 2017a). Some fossil sites were revisited and new localities with vertebrate findings were located, including the “Mateus Quarry”, at Lepidopteris Elv (N71º15.584’ W22º31.785’, 167 m asl - middle Malmros Klint Mb, ~211–210 May, Norian), including well preserved cranial and postcranial elements of phytosaurs (Mateus et al. 2016; Marzola et al. 2018). At this site, the holotype and referred material of NHMD Theropoda n. gen. et sp. was found

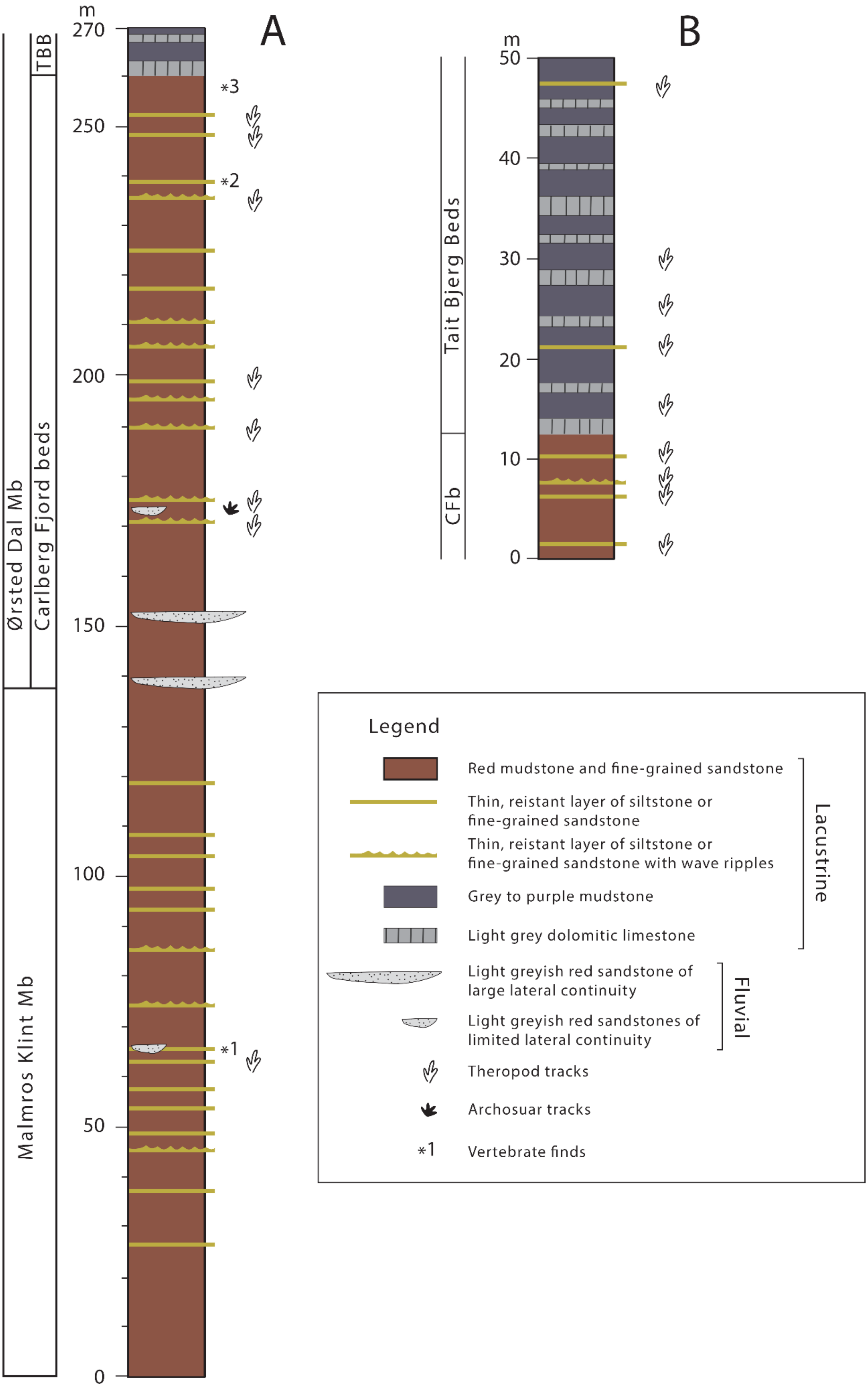

Figure 6.1 – Lithology and track levels at (A) 2016 camp mountain (from Agnolin et al. 2018) and (B) at Track Mountain (Clemmensen, unpublished data). Also indicated the tree main sites with vertebrate remains.

by one of us (OM) on July 13th, 2012. Final preparation of the material has been made by Verena Régent at the Lab facilities of the Dino-Park Münchehagen (Germany).

3D model of NHMD 74732, 195727–31, and 195733–34 have been made through photogrammetry (see Mallison & Wings 2014), using AgiSoft 1.2.0. 1M-face models are available in the Supplementary Material (S6.1–S6.8).

Phylogenetic Analysis

NHMD Theropoda n. gen. et sp. was coded in the data set by Nesbitt and Ezcurra (2015) for a total of 45 taxa and 343 characters, fifteen of which ordered (17, 30, 67, 126, 174, 184, 213, 219, 231, 236, 248, 253, 254, 273, 329, 343) (Appendix A4). On the first analysis, we coded NHMD Theropoda n. gen. et. sp. merely based on the holotype; we then performed a second analysis, including the referred material. We used TNT 1.5-beta, available at www.lillo.org.ar/phylogeny/tnt (Goloboff and Catalano 2016). Both searches were made with 1000 replications using Wagner trees as starting trees, followed by tree-bisection-reconnection (TBR), retaining 10 trees per replication.

Geological Context

The Late Triassic (235–201 Ma) was an epoch of major transition in global land ecosystems and witnessed the early diversification of dinosaurs and other key groups of archosaurian reptiles, such as crocodylomorphs and pterosaurs (e.g., Brusatte et al. 2010). These groups dominated terrestrial communities for the next 140 Myr. Late Triassic lake deposits of Norian–early Rhaetian age (215–205 Ma) known as the Fleming Fjord Formation are very well exposed along the margin of the Jameson Land Basin in East Greenland. These lake deposits have been the subject of detailed sedimentological and paleontological studies since the late 1970s (e.g., Clemmensen 1980a, b; Jenkins et al. 1994, 1997, 2001, 2008; Clemmensen et al. 1998, 2016; Milàn et al. 2004, 2006, 2012; Hansen et al. 2106; Klein et al. 2016; Lallensack et al. 2017; Marzola et al. 2017b, 2018), with many vertebrate fossils having been collected by joint US-Danish expeditions in the early 1990s. During the Late Triassic, the Jameson Land laid at 40° N (like Portugal modern latitude) and the Fleming Fjord fossils are the Late Triassic vertebrate remains with the highest paleolatitude currently known from the northern hemisphere (Kent and Clemmensen 1996; Clemmensen et al. 1998; Kent and Tauxe 2005; Kent et al. 2014).

Systematics Paleontology

Dinosauria Owen 1842, sensu Padian and May (1993)
Saurischia Seeley 1887
Theropoda Marsh 1881, sensu Gauthier (1986)
NHMD Theropoda n. gen. et sp.
(Figs. 6.2–6.9; S6.1–S6.8)

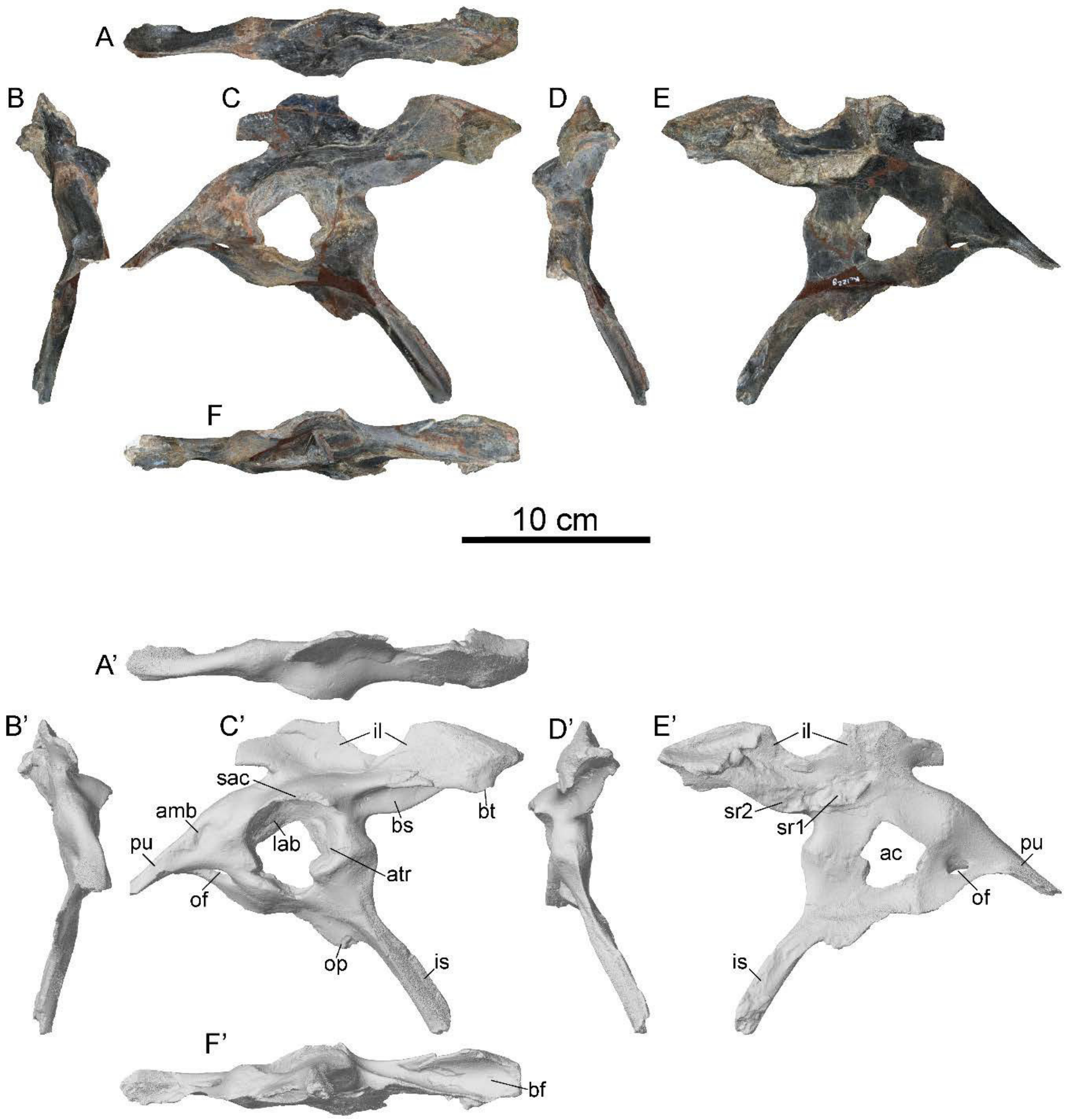

Figure 6.2 - Holotype of NHMD Theropoda n. gen. et sp., NHMD 74732, left pelvis in A, dorsal; B, posterior; C, lateral; D, anterior; E, medial, and; F, ventral views. A’–F’ are digital models of NHMD 74732. Abbreviations: **ac**, acetabulum; **il**, ilium; **is**, ischium; **ob**, obturator foramen; **pu**, pubis

Holotype: NHMD 74732, Articulated and fused left pelvis (ilium, pubis and ischium) only missing both pubic and ischial distal end, and a portion of the iliac anterodorsal margin (Fig. 6.2; S6.1)

Referred material: NHMD 195727, a left scapula; NHMD 195728, a right femur; NHMD 195729, a right femur R; NHMD 195730, a left femur; NHMD 195732, a skull fragment; NHMD 195733, a phalanx; NHMD 195734, a right scapula (Figs. 6.3–6.9; S6.2–S6.8).

Diagnosis of the genus and species: basal theropod with pubis with one foramen and the ischial peduncle with dorsal notch.

Description

Holotype

NHMD 74732 is an articulated, left pelvis, fused, well preserved, nearly complete, with exception for the dorsoanterior part of the iliac blade and the distal end of the pubis and ischium. The pelvic bones are well fused, and the suture is barely visible. There is no fusion with or remains of the sacral ribs but is clear their attachment area in the medial side of the ilium.

Ilium. The ilium is 165 mm long. The dorsoanterior, preacetabular, portion of the iliac blade is not complete so that the exact outline cannot be determined with rigor. One the other hand, the remaining part is well preserved and apparently not distorted.

The brevis fossa is well defined, in the ventral aspect of the postacetabular portion of the ilium, increasing of width posteriorly. The medial margin of the brevis fossa is not fused to the vertebrae, while the lateral lamina gently merges with the supraacetabular crest making a continuity between these two structures: lateral margin of the brevis fossa and the supraacetabular crest. Still, such rim makes a gentle lateral concavity. This deep brevis fossa, for the attachment of the M. caudofemoralis brevis is facing ventrally on the ventral surface of postacetabular part of the ilium, with the brevis shelf margin oblique, positioned anteriorly from the base of the ischial peduncle of the ilium to the posterior-most corner of the ilium. In the lateral face of the postacetabular blade there is a curved ridge connecting from the brevis tuberosity to the posterodorsal margin of the ilium.

The iliac blade is concave laterally and straight medially, as an anteroposterior elongated vertical plate. In anterior view the blade is vertical and all pelvis in just 40 mm wide, with the maximum expansion at the supraacetabular crest. The surface is smooth and regular, except for the distal end which bears a triangular rugosity that is gently projected laterally.

The anterior preacetabular process extends anterior of the acetabulum but less than the pubic boot. The anterodorsal corner of the ilium in broken and absent therefore the outline and shape of the anterior preacetabular portion cannot be determined. The postacetabular process tapers distally, with ventral and dorsal margins being nearly parallel at the posterior portion. Its lateral surface is distinctively convex laterally in its posteriormost part, where two fossae separate by a narrow, anteroposterior crest are evident on its dorsal surface, while the ventral surface is strongly concave all along its anteroposterior axis. The posteroventral margin is nearly horizontal, which angles posterodorsally towards to posterior-most corner of the ilium, forming a 140º angle. The posteroventral margin, from this angle to the posterior end of the ilium, is slightly concave or notched in lateral view.

The acetabulum is round and wide representing about one third of the iliac length. The supraacetabular crest caps the entire portion of the acetabulum with a round roof (slightly damaged at the anterior most rim). In dorsal aspect, the supraacetabular crest of the lateral lamina of the brevis fossa occupy a relevant body in dorsal view. The supraacetabular crest forms a dorsal shelf, convex dorsally and concave ventrally, as an awning occupying all the laterodorsal aspect of the acetabulum. The supraacetabular crest extends anterodorsally to the same length of the acetabulum, anteriorly close to the pubic peduncle and posteriorly in a more dorsal position, at the base of the ischial peduncle.

Caudally, the ilium tapers distally and forms a shallow distal notch facing posteroventrally. The posterior and dorsal margin is occupied by a lateral tuberose crest for the attachment of musculature. The acetabulum is open, forming a well-defined triangular gap in the ilium. In inside of the acetabulum in concave in the ilium and ischium and flattened in the pubis. The ventral and dorsal margin of the acetabulum and concave. The anti-trochanter (sensu Tsai et al. 2018, but not sensu Romer 1956) is present in both ilium and ischium.

The pubic peduncle and the preacetabular lamina for a 20° angle notch. The pubic peduncle is significantly larger than the ischial one. The pubic peduncle is projected anteroventrally and is confluent with the pubic, so that the anterior margin is straight, being slightly bowed near the suture. The iliopubic suture forms an angle of 70–80 degrees with the main axis of the iliac body, so the attachment is mainly facing anteriorly.

The ischial peduncle of the ilium is triangular in cross section, being anteroposteriorly longer than wide or deep. This peduncle is projected ventroposteriorly from the tail portion of the supraacetabular crest, well expanded posteriorly to the anterior margin of the postacetabular embayment.

Pubis. The pubis is fused both to the ilium and ischium, with the distal end missing. The preserved length is 85 mm. Proximally, it is 24 mm wide and distally is 21 mm in width. The pubis long axis is oriented anteroventrally. The iliac peduncle and the acetabulum form a continuous straight line. There is a dorsal notch in the ischial peduncle of the pubis that separates the contact with the ischium from the acetabular anteroventral face, probably for contact of the pubofemoral ligament (see Tsai et al. 2018). The pubic posterior blade contacts with the ischium alongside the whole posterior margin. The ventral margin is horizontal and converges with the pubic shaft with no distinct ventral notch. There is a single, closed, elliptical obturator foramen, which is longer axially than vertically deep. The obturator foramen forms a channel that is oriented mediodorsally to ventrolaterally. The lateral facet of the pubis is flattened while the medial facet of the pubic shaft bears a longitudinal distinct crest, the pubic apron, that contacts the antimere pubis. The pubic apron anteroposterior thickness is constant, with the proximal portion like the rest of the pubic apron. At its distal breakage, the shaft bears a comma-shape outline, being wider transversally than long axially. The shaft anterior facet is convex while the posterior one is concave. The prepubic process is absent so the anterior margin is not expanded.

Ischium. The preserved ischium is 122 mm long and misses the distal end. The ischium long axis is oriented posteroventrally. The pubic peduncle of the ischium is strongly pronounced and forms a neck that separates the main ischial body. The iliac facet and the acetabular antitrochanter facet are nearly confluent but still forming a gentle angle. The shaft is straight to slightly bowed ventrally. The crossed section of the shaft is subtriangular, flatten medially, and one of the vertice laterally, which weakens progressively distally. The obturator process is a vertical flange that project ventrally, rounded in its lateral outline. The obturator notch is confluent with the pubic peduncle, dorsally, forming a gently concave rim, while ventrally from a notch, separated from the shaft.

Referred material

Cranial

Jugal. The left jugal NHMD 195732 is 30 mm in length along its ventral margin, 25 mm in height, and 5 mm thick. The bone is complete but very fragile, therefore preparation along the edges could not be completed, leaving some details concealed. Its outline is elongated, V-shaped, with a short ventroposterior ramus and a longer dorsal ramus. The long axis of the body is nearly horizontal, and its lower margin presents a flange projecting ventrally on the anterior half. The anterior end is round, with interdigitated sutures. The existence of the maxillo-lacrimal contact is unclear, so that the participation of the jugal to the antorbital fenestra cannot be assessed. The lateral surface bears four foraminae plus a bulgy, longitudinal ridge running from the anterior part of the anterior projection to the anterior margin of the postorbital fenestra. In the anterior section, there is no evident slot-like gap for the maxilla. The anterodorsal curvature is gentle, without a horizontal anterior portion. The postorbital projection is 22 mm long and likely tapers anterior to the postorbital. The terminal posterior session flares medially. The

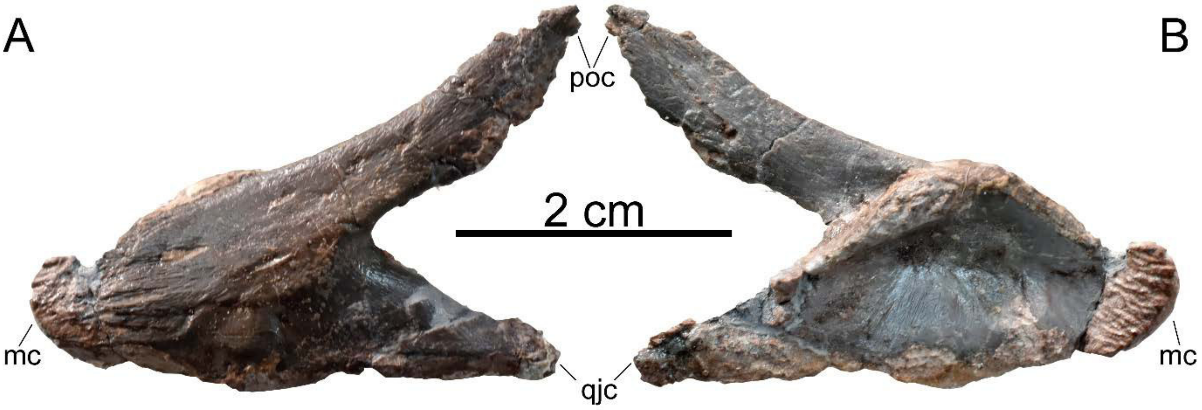

Figure 6.3 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195732, left jugal in A, lateral and; B, medial views. Abbreviations: **mc**, contact with the maxillary; **poc**, contact with the postorbital; **qjc**, contact with the quadratojugal

ventroposterior ramus that contacts the quadratojugal ends acutely and, apparently, overlaying the quadratojugal dorsally. The contact with the quadratojugal is not entirely certain, but the anteriormost part of the contact is at the level of the midlength of both dorsal and posteroventral rami. The lateral side is convex, while medial side is concave. A conspicuous lamina runs from the dorsal border of the anterior projection to the dorsal border of the ventroposterior ramus. The jugal body is tall, its height at the posterior bifurcation is 17 mm. The angle between the two posterior rami is ~45°, so that the jugal would participate to the anterior third of the lower temporal fenestra only.

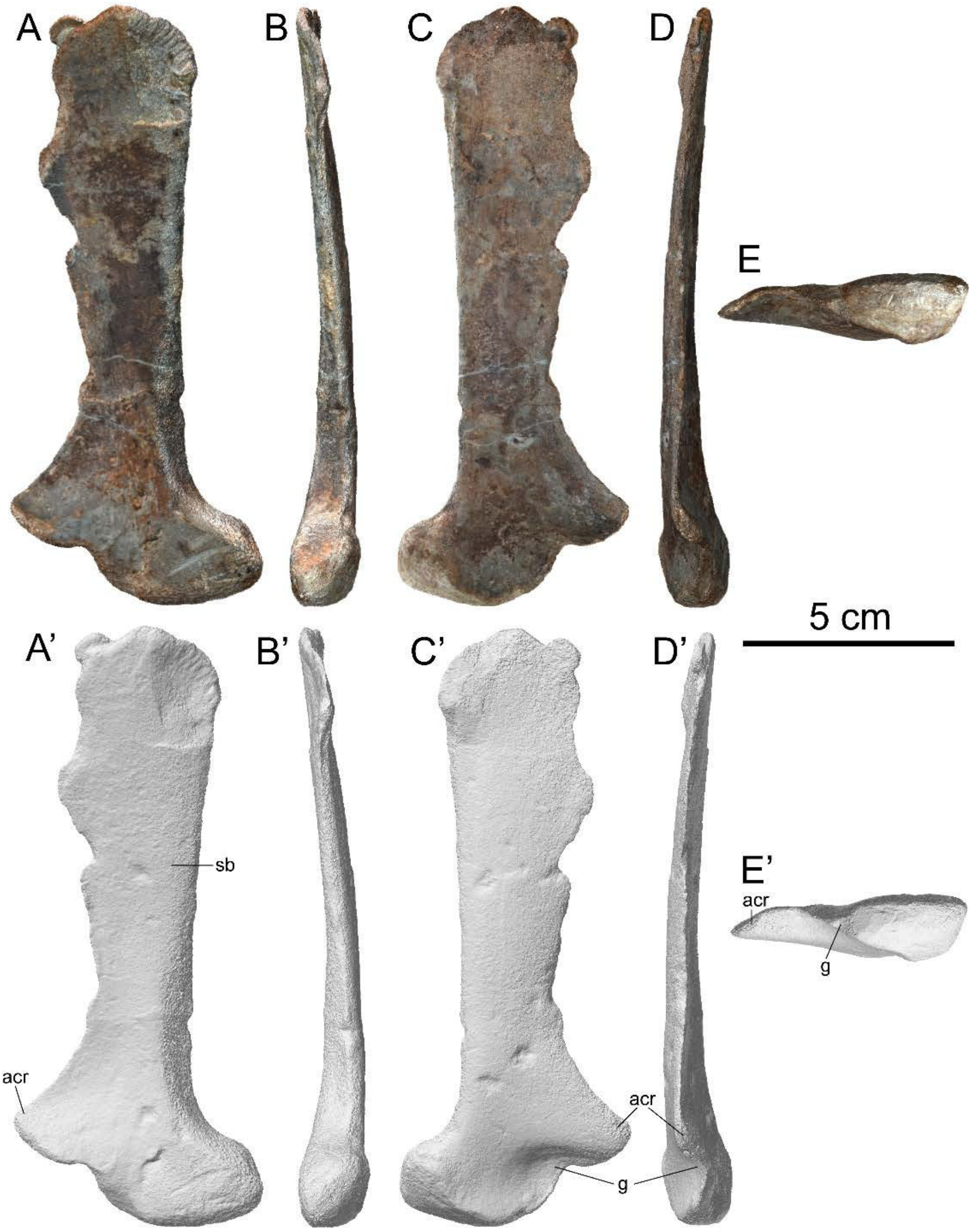

Figure 6.4 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195727, left scapula in A, lateral; B, frontal; C, medial; D, posterior, and; E, ventral views. A'–E' are digital models of NHMD 195727. Abbreviations: **acr**, acromion; **g**, glenoid; **sb**, scapular blade

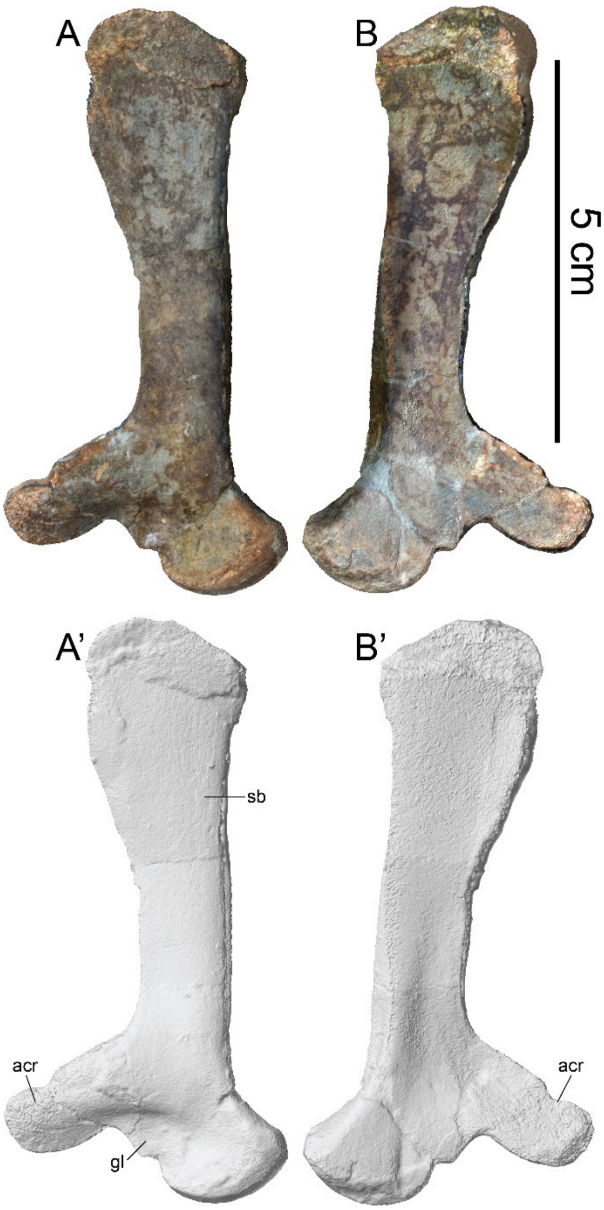

Figure 6.5 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195734, right scapula in A, medial, and; B, lateral views. A’–B’ are digital models of NHMD 195734. Abbreviations: **acr**, acromion; **g**, glenoid; **sb**, scapular blade

Postcranial

Scapulae. NHMD 195727 (Figs. 6.4) is a left scapula. NHMD 195734 (Figs. 6.5) is a right scapula.

Femora. The most complete femur associated NHMD Theropoda n. gen. et. sp. is NHMD 195729 (Fig. 6.6), a right femur 193 mm long. It is complete, crushed at the anterior part of the midshaft. The fourth trochanter and the tibial condyle are partly damaged. The shaft is very bowed, sigmoid in axial view. The maximal extension of the proximal end 32 mm laterally and the femoral head is 23 mm tall. In proximal view, the head is wedged-shaped with the head end being the most expanded section. The posterior side of the head bears a vertical furrow (=ventral emargination) and both the anteromedial and the posteromedial tubera, which give an asymmetrical outline in proximal view. The anteromedial tuber is small, rounded and projects anteriorly at the same level than the posteromedial tuber, a smooth, gently rounded lump larger than the former. The proximal end is smoothly round. The anterior facet of the mediodistal corner of the femoral head presents a round, ventral emargination round fossa, mediodistally to the anterolateral tuber. The lesser trochanter is well developed as an anterior, broaden, vertical lamina projecting anteriorly and connecting with the femoral head without an appreciable notch. The proximal-most position of the anterior trochanter is slightly proximal to the femoral head distal end. There is a second, vertical crest in the anterolateral corner of the proximal end of the femur, parallel to the lesser trochanter. This crest forms with the lesser trochanter a shallow furrow and is also present in the left femur NMHD 195730 and is potentially autapomorphic. This crest is only 8 mm long and projects 2 mm above the lesser trochanter. The anterior facet above the lesser trochanter is flat and is bordered medially by an oblique ridge, from which the femoral head curves medioposteriorly. The mediodistal

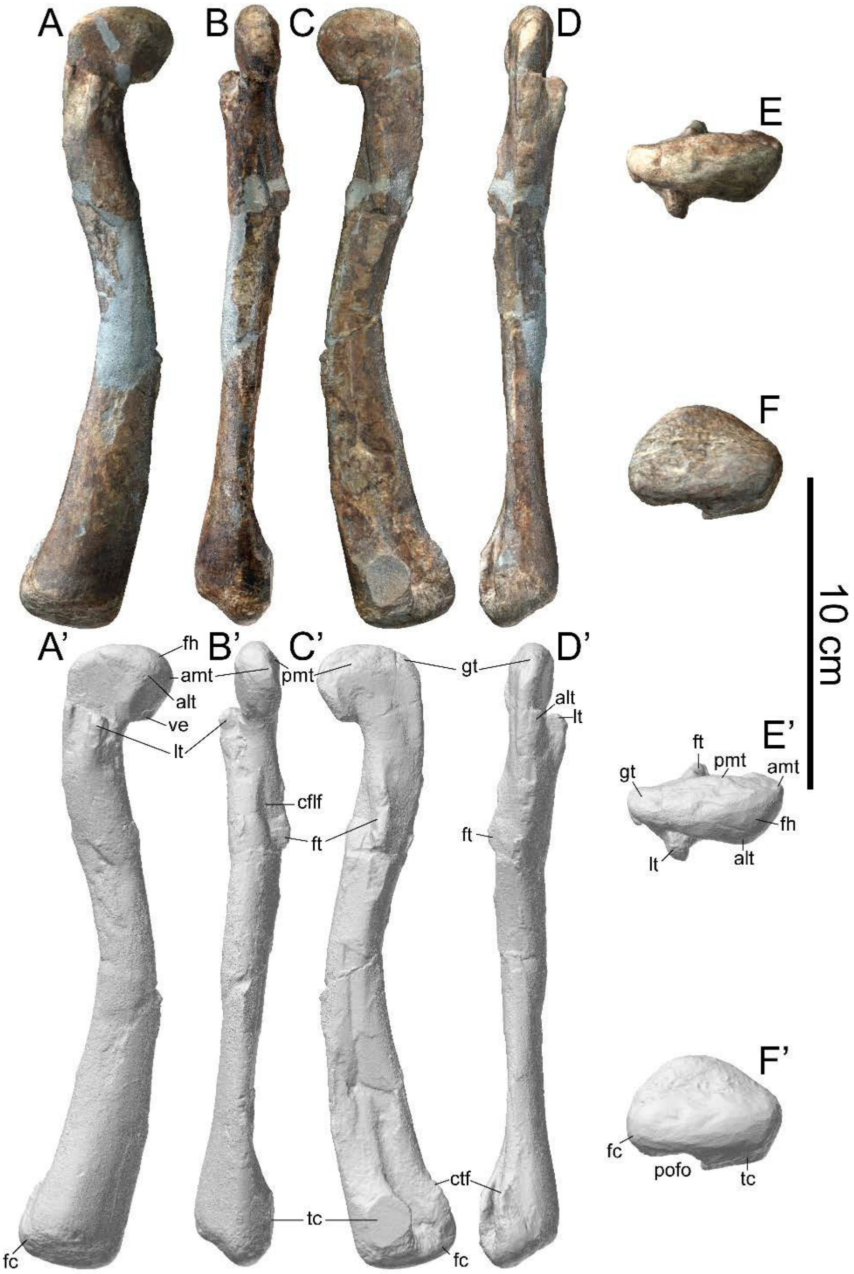

Figure 6.6 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195729, right femur in A, anterior; B, medial; C, posterior; D, lateral; E, dorsal, and; F, ventral views. A'–F' are digital models of NHMD 195729. Abbreviations: alt, anterolateral tuber; **cflf**, caudofemoralis longus fossa; **ctf**, crista tibiofibularis; **fc**, fibular condyle; **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **lt**, lesser trochanter; **pofo**, popliteal fossa; **pmt**, posteromedial tuber; **tc**, tibial condyle; **ve**, ventral emargination

corner of the femoral head forms an obtuse angle posteriorly, between a sub-horizontal distal rim and an inclined medial facet. The femoral head is oriented medially. The fourth trochanter is a sharp, dorsoventrally asymmetrical ridge. In posterior view, it runs proximomedially to distolaterally along the femoral shaft along 40 mm within the proximal half of the femoral shaft, below the lesser trochanter. The caudofemoralis longus fossa is a shallow, vertical groove on the medial side of the proximal half of the fourth trochanter. The minimum diaphyseal thickness (measured along the anteroposterior axis)

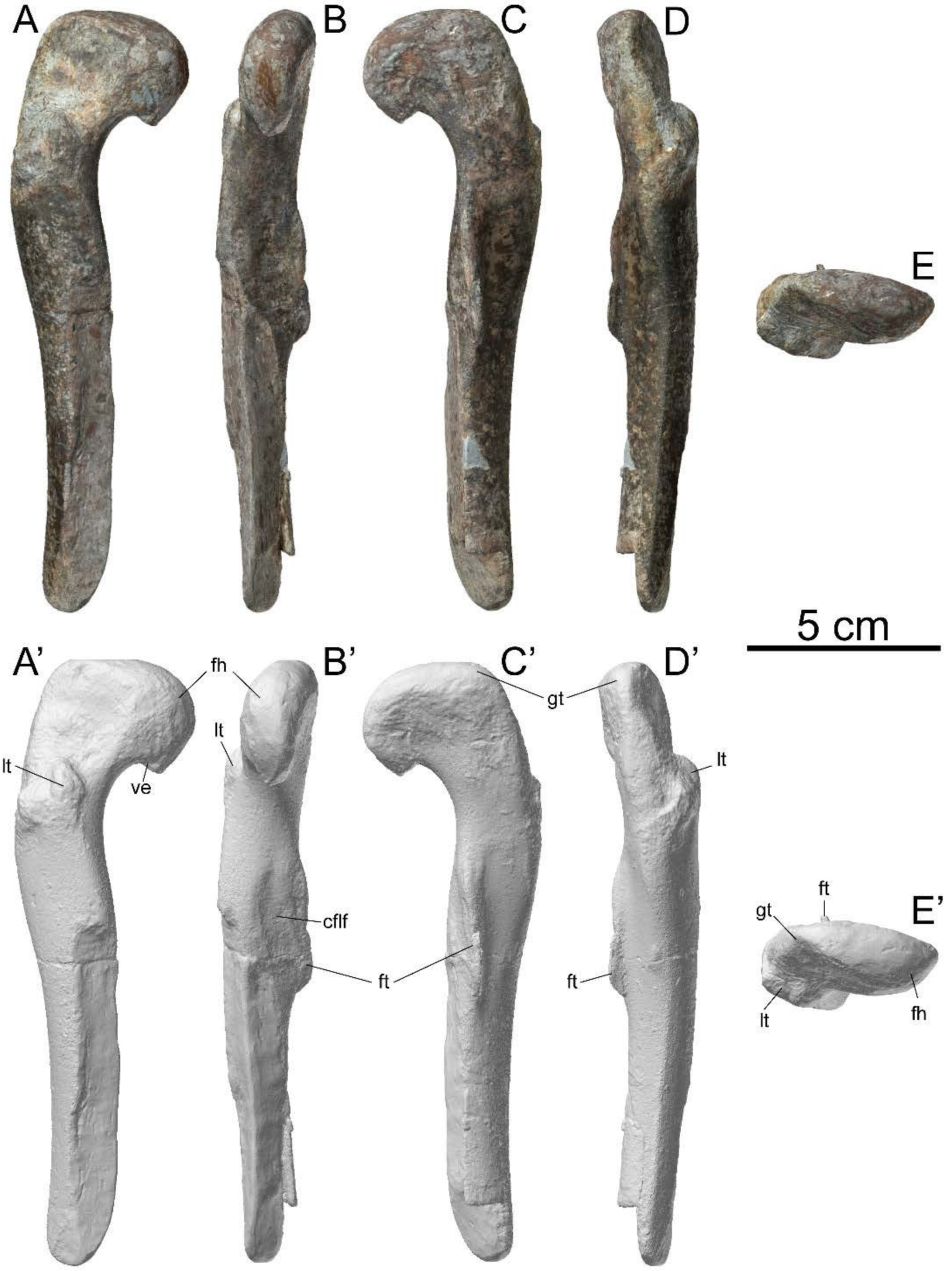

Figure 6.7 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195728, right femur in A, anterior; B, medial; C, posterior; D, lateral, and; E, dorsal views. A’–E’ are digital models of NHMD 195728. Abbreviations: **cflf**, caudofemoralis longus fossa; **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **lt**, lesser trochanter; **ve**, ventral emargination

diaphyseal is 11 mm, while the minimum diaphyseal perimeter is 53 mm at midshaft which, in cross section, is sub-round to ellipsoid, wider transversely than anteroposteriorly. From there, the femur broadens considerably, so that the distal end is massive and robust, 31 mm transversally and 30 mm anteroposteriorly. The distal half of the femur has an edge shape in anterior view, with linear lateral and medial sides, without significant abrupt expansion. The anterior facet is smooth and hemicylindrical. The posterior facet is flat to concave, due to the intercondylar groove that stands for at least 35 mm. The tibial condyle is at least twice the size of the fibular condyle, and both project posterolaterally. The crista

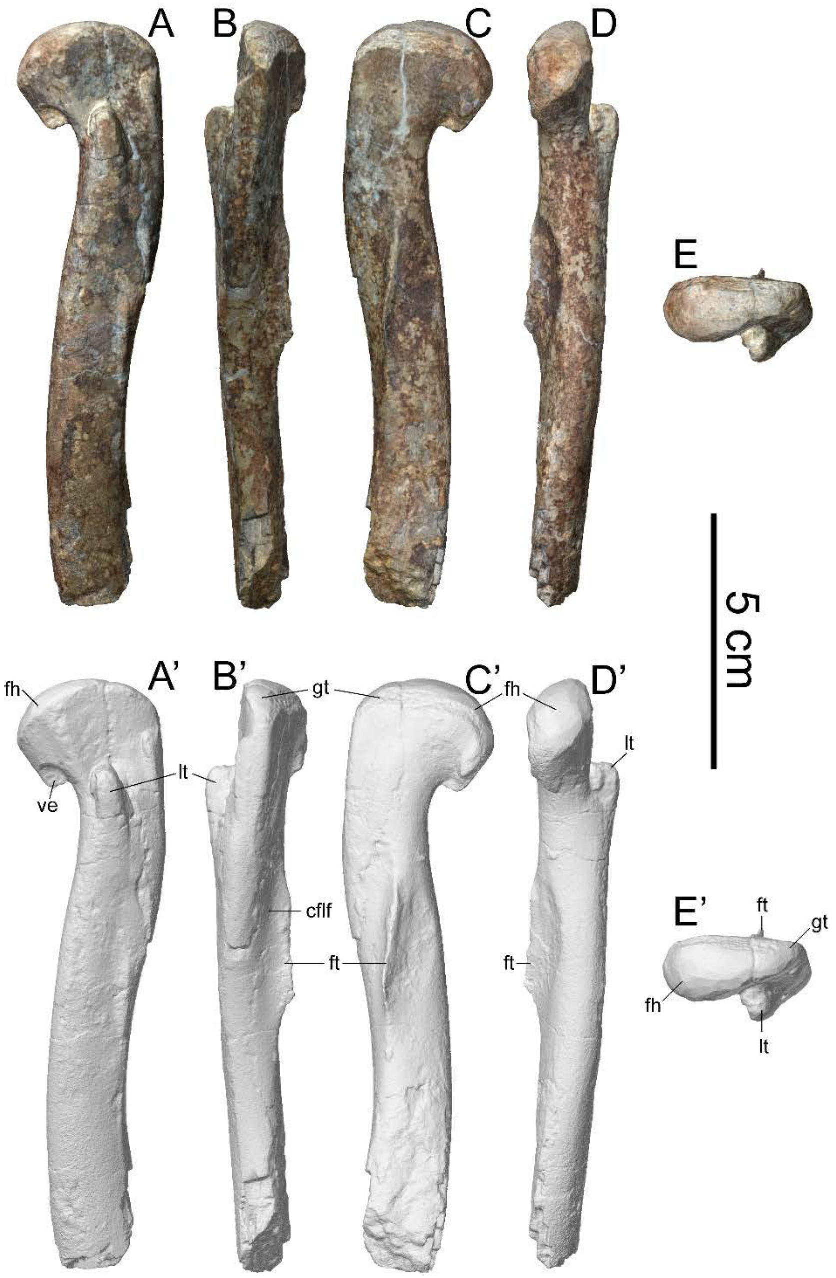

Figure 6.8 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195730, left femur in A, anterior; B, lateral; C, posterior; D, medial, and; E, dorsal views. A'–E' are digital models of NHMD 195730. Abbreviations: **cflf**, caudofemoralis longus fossa; **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **lt**, lesser trochanter; **ve**, ventral emargination

tibiofibularis is mostly appreciable in posterior view and inserts into the fibular condyle with an obtuse angle in distal view. The distal intercondylar anatomy is unclear because, distally, the bone and the matrix become indistinguishable, making it hard to access the shape.

NHMD 195728 is a right femur preserved only as proximal half (Fig. 6.7). It presents one main difference to NHMD 195729, besides the larger size, or that the lesser trochanter is a mound-like projection that coalesces with the trochanteric shelf. NHMD 195729 does not present the round fossa in the anterior facet of the mediodistal corner of the femoral head, nor the vertical secondary crest as in

NHMD 195729 which, on its turn, does not present a trochanteric shelf. These differences are coherent with the dimorphism of *Coelophysis rhodesiensis* Raath 1969 (see also Raath 1977, 1990).

NHMD 195730 is a left femur preserved as proximal half (Fig. 6.8). Its anatomy is consistent with the description of NHMD 195729, except for two differences: i. the fourth trochanter is complete and preserved as a thin, acute lamina running dorsomedially to anteriorventrally, so obliquely, along the posterior face of the femur; ii. the femoral head projects more distally, thus forming a notch with the shaft.

Phalanx. NHMD 195733 is a right (?) phalanx (Fig. 6.9).

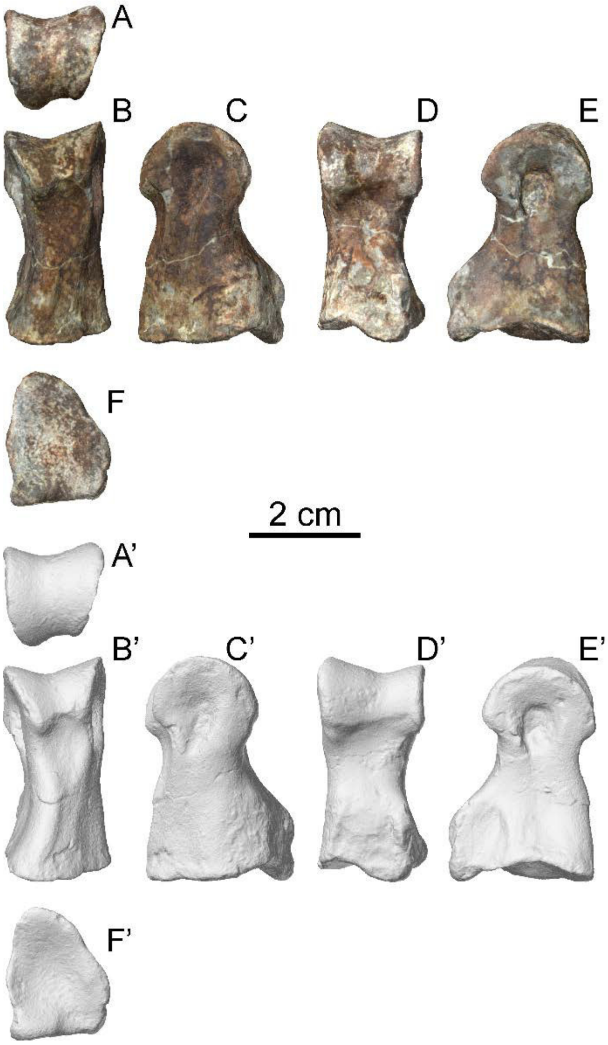

Figure 6.9 - Referred material to NHMD Theropoda n. gen. et sp., NHMD 195733, right? phalanx in A, anterior; B, dorsal; C, lateral; D, ventral; E, medial, and; F, posterior views. A'–F' are digital models of NHMD 195733

Taphonomy

The pelvis was found isolated, nearly intact, undamaged, within a fine sandstone. Besides being isolated, there is no other signs of taphonomical transportation. The pelvis was recovered during the dig of the phytosaur bonebed with four individuals of three size-classes. In one single quarry were collected four individuals of three different size-ranges. Most bones are from an adult or sub-adult (3.5 m long). Three complete dorsal neural arches and one centrum, all with unfused open neurocentral suture, and an anterior part of a dentary about 63 mm long show an additional presence of an animal of about one to two meters of body length. The third and smaller body size is deduced from one complete left scapula with only 34 mm long. This size suggests a body length of 45 to 55 cm. This assemblage of five predators in a single well confined bonebed is even more bizarre when they represent the extremely rare taxa, being only reports of both phytosaurs and theropods in all Greenland. This is hardly a coincidence and several hypotheses can be discussed: i) mud-trap / quick-sand; ii) last water resource in the area after drought; iii) cold-wave; iv) carcasses concentration by water currents.

i) mud-trap / quick-sand: In favor to this hypothesis is the fat that is well known to occur in the fossil record (i.e., Miller 1971; Harris 1985; Clark & Xu 2009; Eberth et al. 2010; Schoch & Seegis

2014; Sereno 2014;) and modern situation. It is consistent with the sedimentology (mud and fine sandstone). The bonebed is consisted by carnivorous-only taxa, which may be have be attracted by the carcass smell.

ii) last water resource in the area after drought: well known to happen in the Triassic in which animals concentrate in large numbers (e.g. Brusatte et al. 2015) in the last remain of water during a severe drought. There are several documented cases, mainly for temnospondyls. Against this hypothesis is the kind of fauna: agile carnivores only, that could travel long distances.

iii) cold-wave

iv) carcasses concentration by water currents: in most cases the bones were not articulated suggesting some transportation. But a wider spread rather than a concentration would be expected.

No definitive explanation can be proven but to the light of the nowadays rationale and knowledge, the hypothesis of a mud-trap / quicksand that imprisoned the phytosaurs and theropod is the one that better explains the data and observations.

Discussion

Phylogenetic results

The first analysis, including the only holotype of NHMD Theropoda n. gen. et sp. led to eight most parsimonious trees, with a length (TL) of 1064 steps, consistency index (CI) of 0.385, retention index (RI) of 0.676 and a rescaled consistency index (RCI) of 0.260 (Fig. 6.10A). The best score was hit 477 times out of the 1000 replications.

The second analysis, including also characters coded in NHMD Theropoda n. gen. et sp. referred material, gave 32 most parsimonious trees, with a TL of 1076 steps, CI of 0.381, RI of 0.672 and RCI of 0.256 (Fig. 6.10B). The best score was hit 723 times out of the 1000 replications.

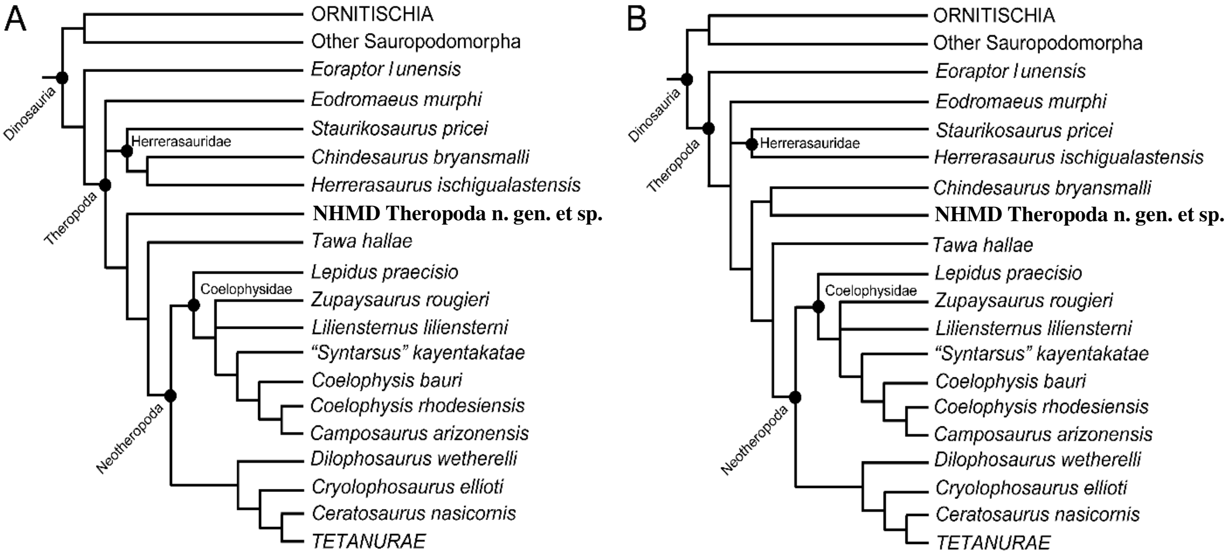

Figure 6.10 - Phylogenetic relationships after Ezcurra & Martínez (2016) and Ezcurra (2017)

In the first analysis, the holotype only (left pelvis) of NHMD Theropoda n. gen. et sp. was recovered as a the basalmost known theropod, with the New Mexico taxon *Tawa hallae* Nesbitt *et al.* (2009) and the Coelophysidae as its closest relatives (Fig. 6.10A). However, including the coding from the referred material (jugal, scapula, and femur), NHMD Theropoda n. gen. et sp. is found as the sister taxon of *Chindesaurus bryansmalli* Long and Murry 1995, from the Chinle Formation of Arizona. *C. bryansmalli* is considered a herrerasaurid, though in our analysis it brunches with NHMD Theropoda n. gen. et sp. at the base of the Theropoda, outside the Herrerasauridae clade (Fig. 6.10B).

Ontogenetic stages

The pelvic bones are well fused, and the suture is barely visible, showing that is an adult individual.

7. CONCLUSIONS

This thesis highly increases the knowledge on the Late Triassic vertebrate fauna of the Jameson Land Basin, in East Greenland, and its relationship with coeval faunas from Europe and North America. During the Late Triassic, the Central East Greenland laid between 40º and 44º N, at a latitude comparable to modern Portugal and Galicia. The Fleming Fjord Formation is a sedimentary basin made of rocks that record, during the Norian-Early Rhaetian, a large lacustrine system at the Jameson Land Basin. The whole area was characterized by a temperate climate, with an alternation of wet and dry seasons and an abundance of water periodically alternated to drought.

These conditions were optimal for the prosperity of a vertebrate fauna that included all the main groups known at that time, ranging from fish to amphibians, from reptiles to mammals. Besides *Ceratodus tunuensis*, a new sarcopterygian lungfish taxon, this thesis focuses more specifically on the tetrapod taxa. *Cyclotosaurus naraserluki* is a new Greenlandic taxon of amphibian, the westernmost and northernmost capitosaurid ever recovered. Capitosaurids have also been found in Europe, Algeria, and southern USA, but Middle Triassic findings from Western Russia testify their European origin.

Reptiles were dominating the vertebrate ecosystem of the Jameson Land Basin, testified by the presence of both aquatic and terrestrial, as well as herbivore and carnivorous taxa. *Sikuqisik jenkinsi* is a proposed new taxon of herbivor typothoracin aetosaur reppresented by an adult individual. Considering also *Paratypothorax*, a second typothoracin taxon reported from the Jameson Land Basin, this group of armored quadrupedal herbivore reptiles seems to be the only Greenlandic vertebrate with North American origins, as proven by their older closest relatives: *Apachesuchus* and *Redondasuchus* (both from New Mexico, USA) for *S. jenkinsi*; *Rioarribasuchus* and *Tecovasuchus* (from Arizona, Mexico and Texas, USA) for *Paratypothorax*.

NHMD Testudinata n. gen. et sp. (proposed taxon) was one of the semiaquatic Testudinata living in the fresh waters of the lake at the Jameson Land Basin. Straightly related to the Central European *Proganochelys*, NHMD Testudinata n. gen. et sp. might not have been the only distinct Testudinata taxon from Central Eastern Greenland, with two more specimens here briefly reported and yet under study.

Covering a similar ecological niche to modern crocodiles, phytosaurs ruled the costs of the seasonal Late Triassic lake in East Greenland, having probably a reproductive and living terrestrial life, with aquatic predation. With this thesis, a lot of 3D material and a preliminary anatomical analysis are given about six phutosaur individuals from the Jameson Land Basin, represented at least by four adults, one sub-adult, and a juvenile.

3D material is also provided for sauropodomorph dinosaurs, yet at a primordial stage of research and here reported as two adults and one sub-adult, with skulls and postcranial material. The real rulers of the terrestrial environments around the Jameson Land Basin were bipedal carnivorous theropod dinosaurs. This thesis reports the first undisputed bone remains of a new Greenlandic theropod taxon, which origins are somewhat dubious, being both related to North American and European taxa. The evolutionary advantage of theropod dinosaurs based on their high activity is potentially supported by the richness theropod tracks and trackways from Jameson Land Basin, recorded by the thousands and probably left during long patroling of the areas aroud the lake searching for preys.

Despite the geographic position of Greenland as part of the North American plate, its Late Triassic fauna shows strong European affinities. During the Late Triassic, North American findings are from the Southern USA, at a tropical paleolatitude of 5–10ºN, while most European findings are from a temperate paleolatitude of 34–44ºN (Fig. 7.1) (Golonka 2007; Golonka et al. 2018; Tanner 2018). The Jameson Land Basin laid at about 40–44ºN during the Late Triassic, preserving some of the Northernmost vertebrate fossils from the Late Triassic (Kent & Clemmensen 1996; Clemmensen et al. 1998; Kent & Tauxe 2005; Kent et al. 2017). Besides the geographical closeness between Greenland and Europe during the Late Triassic, climate had an important rule in the distribution of the faunas. The Hadley cell is responsible of a more arid region from 5–20ºN, laying right between the North American and European fossil sites also during the Late Triassic, and being responsible of a strong and differenciate provinciality between the faunas of the two areas (Fig. 7.1) (Whiteside et al. 2011). During the Late Triassic, Greenland was climatically divided by North America and more closely and easily accessible for faunal interactions from and to Europe. The dispersal of Triassic life was therefore strongly inluenced by paleolatitudinal climate belts. Late Triassic was a warmer time than today, with temperatures supposedly higher up to 6 ºC in average (Sellwood & Valdes 2006; Whiteside et al. 2011).

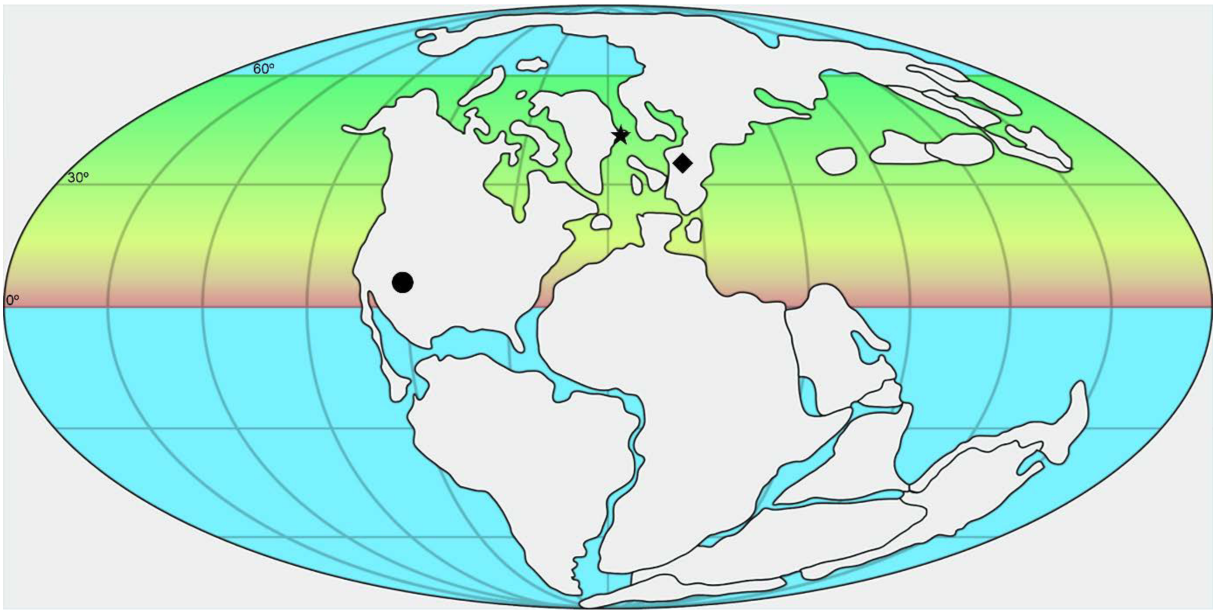

Figure 7.1 – Paleogeographic map of the Late Triassic Pangaea (after Tanner 2018) showing the positions of Greenland (star), Europe (square), and Southern USA (circle) fossil locations. The colored belt is a gradient of different climates, depending on Hadley cell atmospheric circulation, with green corresponding to temperate, yellow subtropical, and red tropical climates.

The Jameson Land Basin was charcaterized by a vast, fresh water lake-mudflat ecosystem, with recorded seasonality and an overall climate that resambled modern Northern-Central Iberian Peninsula, but with seasonal precipitations (Clemmensen et al. 1998, 2016, pers. comm. 2019; Marzola et al. 2017a, b; Mateus et al. 2014).

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APPENDICES

A1 – Character coding for *Cyclotosaurus naraserluki*

Character coding scores for the 69 characters of Witzmann et al. (2016).

Cyclotosaurus naraserluki

01010 0220[0,1] 11?10 01201 01020 1110? 1110? 11111 ????? ??111 ?0?20 01011 1?0?0 1011

A2 – Character coding for *Sikuqisik jenkinsi*

Character coding scores of the 83 characters of Parker (2016).

????? ?10?1 ?10?1 111?1 02??? ????? 01122 ???01 0000? ????? ?1110 ?0??? ??0?0 ????? ?1??? ????? ???

A3 – Character coding for NHMD Testudinata n. gen. et sp.

Character coding scores of the 280 characters of Li et al. (2016).

????? 210?? ????? ??0?? ?01?0 11010 01??? ????? ????? ????? ????? ?11?? ????[12] 11?[?0]? ???1? 11?21 ?1??? ??11?

A4 – Character coding for *NHMD Theropoda n. gen. et sp.*

Character coding scores of the 343 characters of Brusatte and Ezcurra (2015).

Holotype NHMD 74723 only

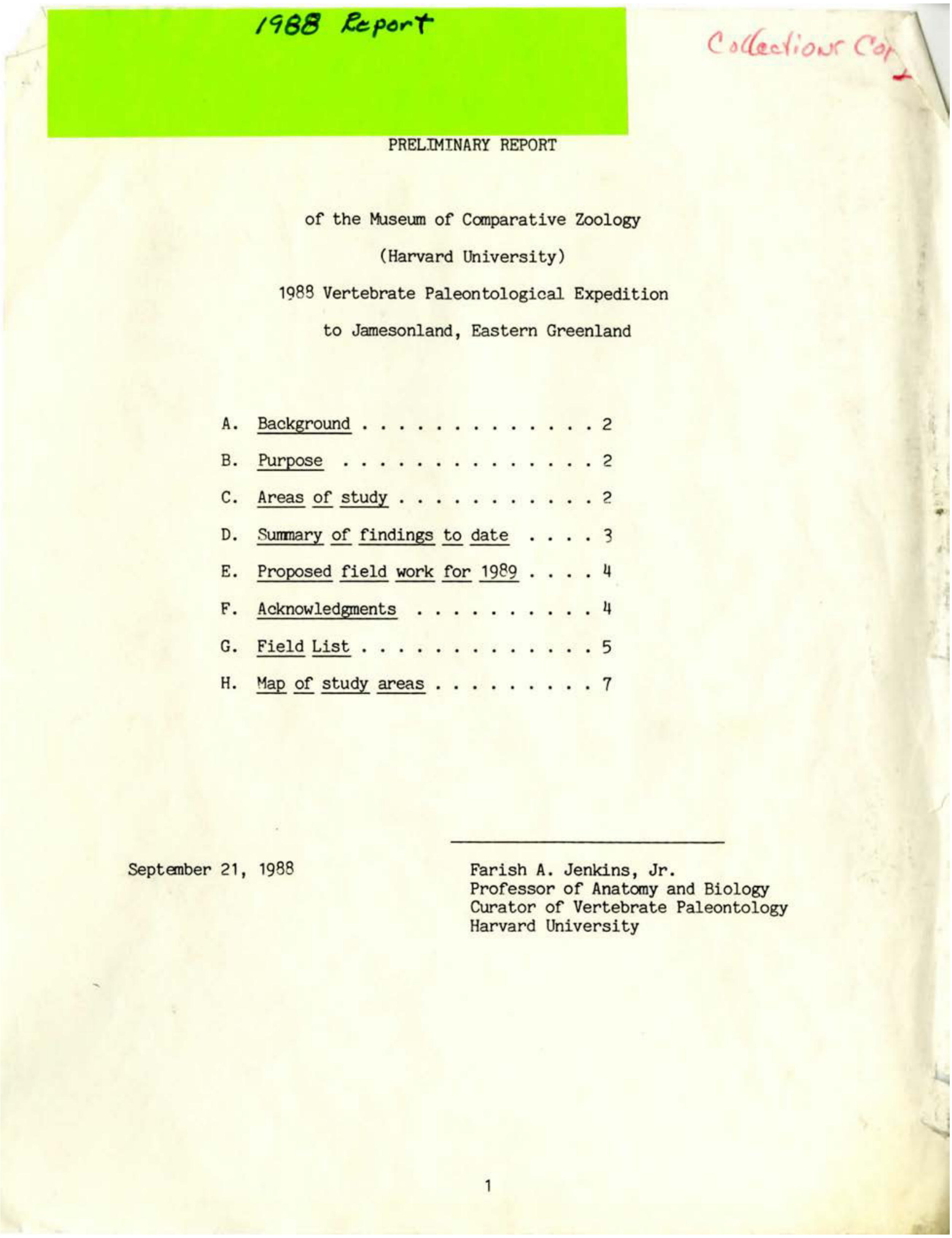
????? ???00 01?10 21210 01?00 ????1 00012 ?0121 1???? ????? 1???? ????? 1??

Referred material

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?0??0 03??? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ??01? ???1? ????? ????? ????? ????? ????? ???00 01?10 21210 01?00 ????1 00012 ?0121 1?110 02210 10110 01110 ?0100 00??? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????0 1???? ????? 1???? ????? 1??

A5 – Field report 1988 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1988 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



1988 Report

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PRELIMINARY REPORT

of the Museum of Comparative Zoology
(Harvard University)
1988 Vertebrate Paleontological Expedition
to Jamesonland, Eastern Greenland

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September 21, 1988

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Professor of Anatomy and Biology
Curator of Vertebrate Paleontology
Harvard University

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A. Background

The 1988 Vertebrate Paleontological Expedition to Eastern Greenland was conducted with the financial assistance of a research grant from the U. S. National Science Foundation (Grant #DPP-87-21757), logistical and technical support from the Polar Ice Coring Office (University of Nebraska, Lincoln), and with the permission of the Kommissionen For Videnskabelige Undersogelser I Gronland. The expedition operated in the field for 31 days from 30 June through 1 August, 1988, and was staffed by Professor Farish A. Jenkins, Jr., Mr. Charles R. Schaff, and Mr. William W. Amaral (all of Harvard University), and also by Dr. Neil H. Shubin (formerly of Harvard, now at the University of California, Berkeley). This investigation would not have been possible without the extensive sedimentological and stratigraphic analyses undertaken previously by Danish geologists, most notably K. Perch-Nielsen et al. (1972, 1974) and L. B. Clemmenson (1980). We are aware that further lithostratigraphic studies are currently being pursued by Mr. Gregers Dam under the auspices of Gronlands Geologiske Undersogelse and supported by British Petroleum. The MCZ party had the pleasure of meeting Mr. Dam and his colleagues briefly at the beginning of the field season.

B. Purpose.

The project was designed to explore various formations of the Scoresby Land Group in eastern Greenland for fossil vertebrates and other evidence relating to the evolutionary transition in terrestrial faunas that took place during Late Triassic through Early Jurassic times. The scope of the project as originally proposed was somewhat broader, but was redefined during the process of review by the National Science Foundation and by the Commission for Scientific Research in Greenland. For logistical and other practical considerations the field work was further focussed on the Upper Triassic and especially on the Orsted Dal Member, Fleming Fjord Formation, which also offered the geochronological zone of greatest potential interest.

C. Areas of study.

Paleontological reconnaissance was undertaken from four base camps in which the following areas were surveyed; all of the areas (see also Section H: Map of Study Areas) lie in the southern half of the Triassic rift basin as interpreted by Clemmenson, and none include any of his measured or figured sections.

Camp I (1 July - 8 July, 1988). Northern end of Klitdal, including the valley floor northeast of Mt. Skansen, bordered by the Paselv to the east and the Lejrelv to the south and west. In general the exposures here were either low-lying and deeply weathered (Fleming Fjord Formation) or largely covered with talus or tundra (Kap Stewart Formation); in both cases they did not offer conditions suitable for paleontological surface prospecting, although substantial efforts were made to cover an area of approximately ten square miles. Several incomplete dentitions, probably representing fish, and a hybodont-type shark tooth were found.

Camp II (8 July - 18 July, 1988). The western side of the Paselv valley at the head of Carlsberg Fjord, an area bounded to the north by the Lepidoperiselv. Here an extensive exposure of the Fleming Fjord Formation occurs, and in particular the Orsted Dal member and the Tait Bjerg beds. Fossil vertebrate remains were found at numerous levels throughout the section, most often in particular lenses and in localized concentrations. Most specimens recovered from the lower parts of the Orsted Dal Member were associated with cyclothemic siltstones, mudstones and dolomitic limestones, and upon examination in the field appeared to represent fish jaws or skulls. The uppermost part of the Fleming Fjord Formation bears evidence of a more terrestrial regeme, and although relatively limited in the extent of exposure, yielded the most promising evidence of both large (dinosaur-size) and small tetrapods.

Camp III (18 July - 26 July, 1988). The region surrounding the southernmost tributary of the Liaselv, on the west side of Carlsberg Fjord. Here again, as in the Camp II area, extensive exposures of the upper part of the Fleming Fjord Formation are present. Paleontological prospecting in this region, however, was severely hampered by inclement weather, and as a result only one area was intensively surveyed. As in the Camp II area, fossils were found in a variety of facies, with evidence of tetrapods occurring in the uppermost part of the formation.

Camp IV (26 July - 1 August, 1988). The southern end of Klit Dal, an area bounded by Dusen Berg to the west and Ryder´s Elv to the east. This area, although seemingly attractive for paleontological prospecting from inspection via helicopter, in fact turned out to be the poorest of all our localities. The Fleming Fjord Formation here is either substantially covered with skree, or where well exposed gives evidence of conglomerates and other high energy clastics in which fossil vertebrates are seldom present in abundance or in a condition warranting scientific study.

D. Summary of findings to date.

1) Paleontological reconnaissance of the Fleming Fjord Formation has demonstrated that fossil vertebrates occur at a number of levels within the formation, and that vertebrate remains are associated with a variety of lacustrine, fluviatile and subaerial environments. Most fossil localities occur within the middle to upper one-third of the Orsted Dal Member of the Fleming Fjord Formation.

2) Terrestrial tetrapods occur predominantly in red and gray siltstones within the upper Tait Bjerg beds at the top of the Fleming Fjord Formation. Although the quality of bone was quite good, many of the vertebrate remains were incomplete. However, specimens found *in situ* (e.g., 11/88G) showed excellent preservation. At least two taxa, a large prosauropod dinosaur and a large ?rauisuchid thecodont, have been tentatively identified on the basis of incomplete skeletons which include vertebrae as well as limb and girdle components. Skull elements and teeth are rare in terrestrial beds, but the beds that typically yielded these fossils were less extensively preserved in the areas surveyed than the lower stratigraphic units wherein fish remains predominate.

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3) One specimen, which is currently the focus of intensive laboratory work, appears to represent a turtle. If this is confirmed through additional preparation, it will be an extremely important addition to our knowledge of chelonian evolution which, on present evidence, began during Late Triassic times.

4) A number of the fossiliferous localities contained abundant bone fragment assemblages, and appear to differ significantly from the Tait Bjerg bone beds described by Clemmenson (1980).

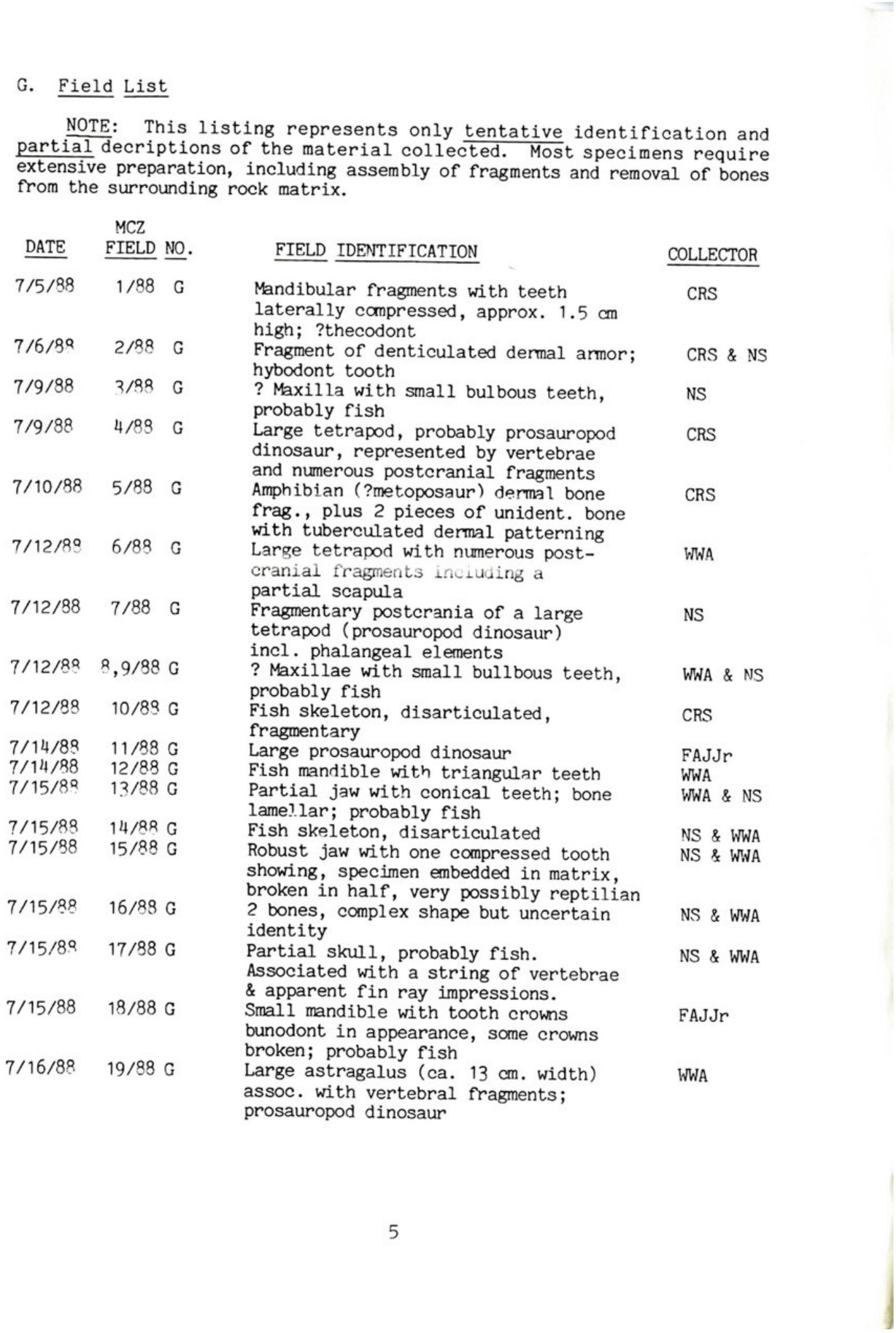
5) All of the specimens collected (Section G, attached) require preparation before further study and a positive identification can be made. Interpretations made of this material at the time of collection, as represented on the Field List, can only be considered tentative.

E. Proposed field work for 1989

Based on the reconnaissance survey accomplished during 1988, we propose that future field efforts be directed toward locating and prospecting additional areas where the Tait Bjerg beds are suitably exposed. This stratigraphic horizon has now been shown to contain a diversity of terrestrial tetrapods which, considered together, are indicative of a late Triassic (Norian) age. We believe that there is good potential for expanding the list of represented taxa, and fulfilling the original goals of the project.

F. Acknowledgments

We are grateful to the Division of Polar Programs (NSF) and its Director, Dr. Herman B. Zimmerman, and The Commission for Scientific Research in Greenland and the Secretary, Mr. Gregers L. Andersen, for their support of this project. In addition we received useful advice during the process of the Commission´s review from Dr. T. C. R. Pulvertaft (GGU), Dr. S. E. Bendix-Almgreen (Geological Museum, University of Copenhagen) and other (anonymous) reviewers. The logistical arrangements and support of the Polar Ice Coring Office and its Field Operations Manager, Mr. Kent Swanson, were essential to our operation. We also wish to express our appreciation for the courteous cooperation of GLACE (Mr. Ole Romer and Mr. Paul Lasson) and AFIS (Mr. Ib Westergaard) in providing excellent transportation and communication services, and to Leading Chief Petty Officer Curtis W. Sattler (U. S. Naval Air Station, Keflavik) for assistance in transferring personnel and cargo through Iceland.



G. Field List

NOTE: This listing represents only tentative identification and partial decriptions of the material collected. Most specimens require extensive preparation, including assembly of fragments and removal of bones from the surrounding rock matrix.

DATE	MCZ FIELD NO.	FIELD IDENTIFICATION	COLLECTOR
7/5/88	1/88 G	Mandibular fragments with teeth laterally compressed, approx. 1.5 cm high; ?thecodont	CRS
7/6/88	2/88 G	Fragment of denticulated dermal armor; hybodont tooth	CRS & NS
7/9/88	3/88 G	? Maxilla with small bulbous teeth, probably fish	NS
7/9/88	4/88 G	Large tetrapod, probably prosauropod dinosaur, represented by vertebrae and numerous postcranial fragments	CRS
7/10/88	5/88 G	Amphibian (?metoposaur) dermal bone frag., plus 2 pieces of unident. bone with tuberculated dermal patterning	CRS
7/12/88	6/88 G	Large tetrapod with numerous postcranial fragments including a partial scapula	WWA
7/12/88	7/88 G	Fragmentary postcrania of a large tetrapod (prosauropod dinosaur) incl. phalangeal elements	NS
7/12/88	8,9/88 G	? Maxillae with small bullbous teeth, probably fish	WWA & NS
7/12/88	10/88 G	Fish skeleton, disarticulated, fragmentary	CRS
7/14/88	11/88 G	Large prosauropod dinosaur	FAJJr
7/14/88	12/88 G	Fish mandible with triangular teeth	WWA
7/15/88	13/88 G	Partial jaw with conical teeth; bone lamellar; probably fish	WWA & NS
7/15/88	14/88 G	Fish skeleton, disarticulated	NS & WWA
7/15/88	15/88 G	Robust jaw with one compressed tooth showing, specimen embedded in matrix, broken in half, very possibly reptilian	NS & WWA
7/15/88	16/88 G	2 bones, complex shape but uncertain identity	NS & WWA
7/15/88	17/88 G	Partial skull, probably fish. Associated with a string of vertebrae & apparent fin ray impressions.	NS & WWA
7/15/88	18/88 G	Small mandible with tooth crowns bunodont in appearance, some crowns broken; probably fish	FAJJr
7/16/88	19/88 G	Large astragalus (ca. 13 cm. width) assoc. with vertebral fragments; prosauropod dinosaur	WWA

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G. Field List (cont.)

7/17/88	20/88 G	Lms nodule with unident. small bone, possible skull	FAJJr
7/17/88	21/88 G	Distal femoral fragment of a large reptile	CRS
7/17/88	22/88 G	Abundant skeletal fragments of a large tetrapod including limb and vertebral elements. ? Chelonian.	WWA
7/20/88	23/88 G *	Fish skull in nodule w/teeth	FAJJr
	24/88 G *	" " " " "	"
	25/88 G *	? fish skull " "	"
7/20/88	26/88 G *	? fish skull	CRS
7/20/88	27/88 G	Bone "conglomerates" mottled maroon limestone	WWA & NS
7/23/88	28/88 G	Amphibian skull fragment	CRS
7/23/88	29/88 G	Large lungfish tooth	WWA
7/23/88	30/88 G	Fish skull	NS
7/26/88	31/88 G	Small bone with some triangular teeth, ?reptile	CRS, FAJJr
7/26/88	32/88 G	Second sample of bone "conglomerate" adjacent to original find of 7/20/88 (27/88 G)	NS, WWA

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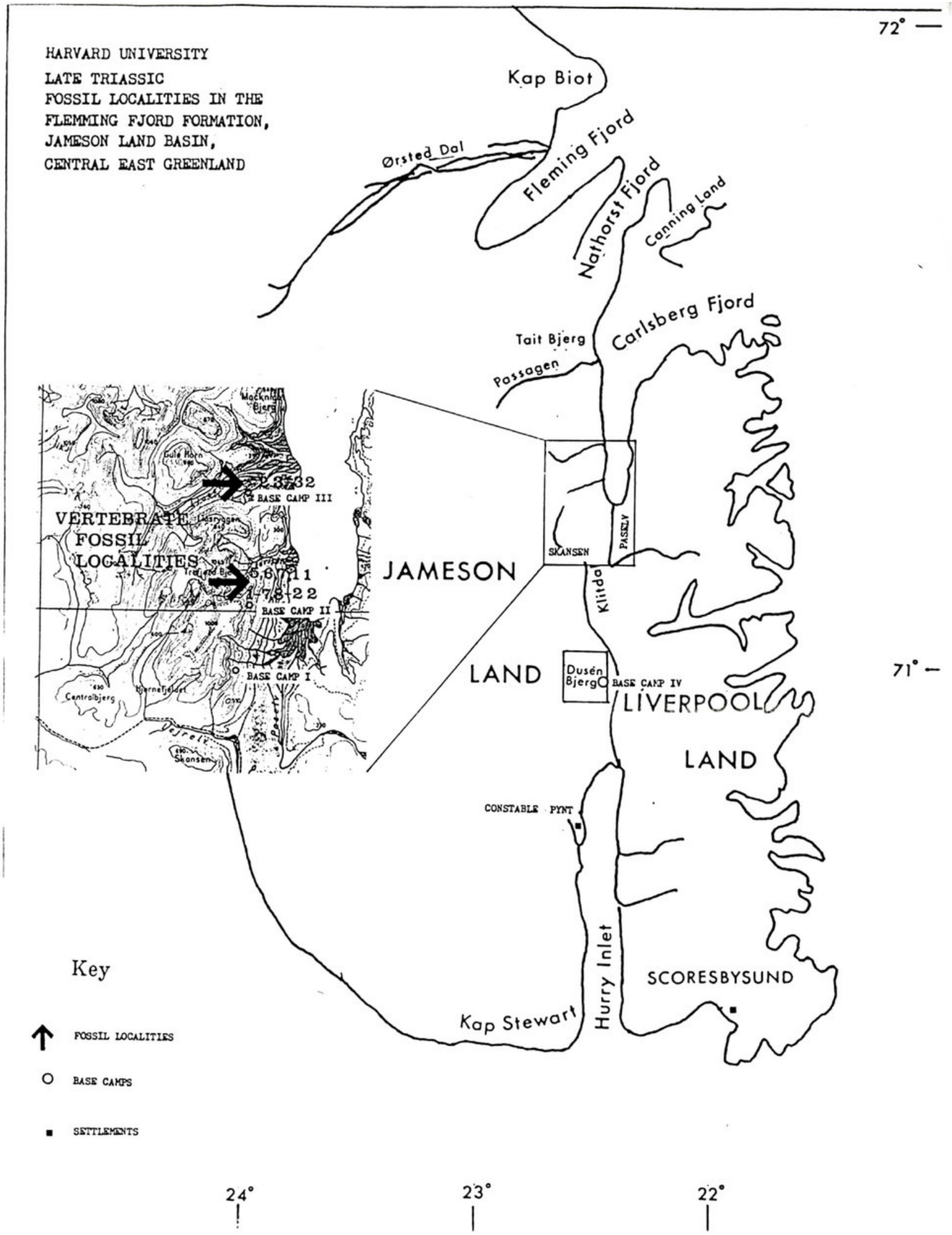
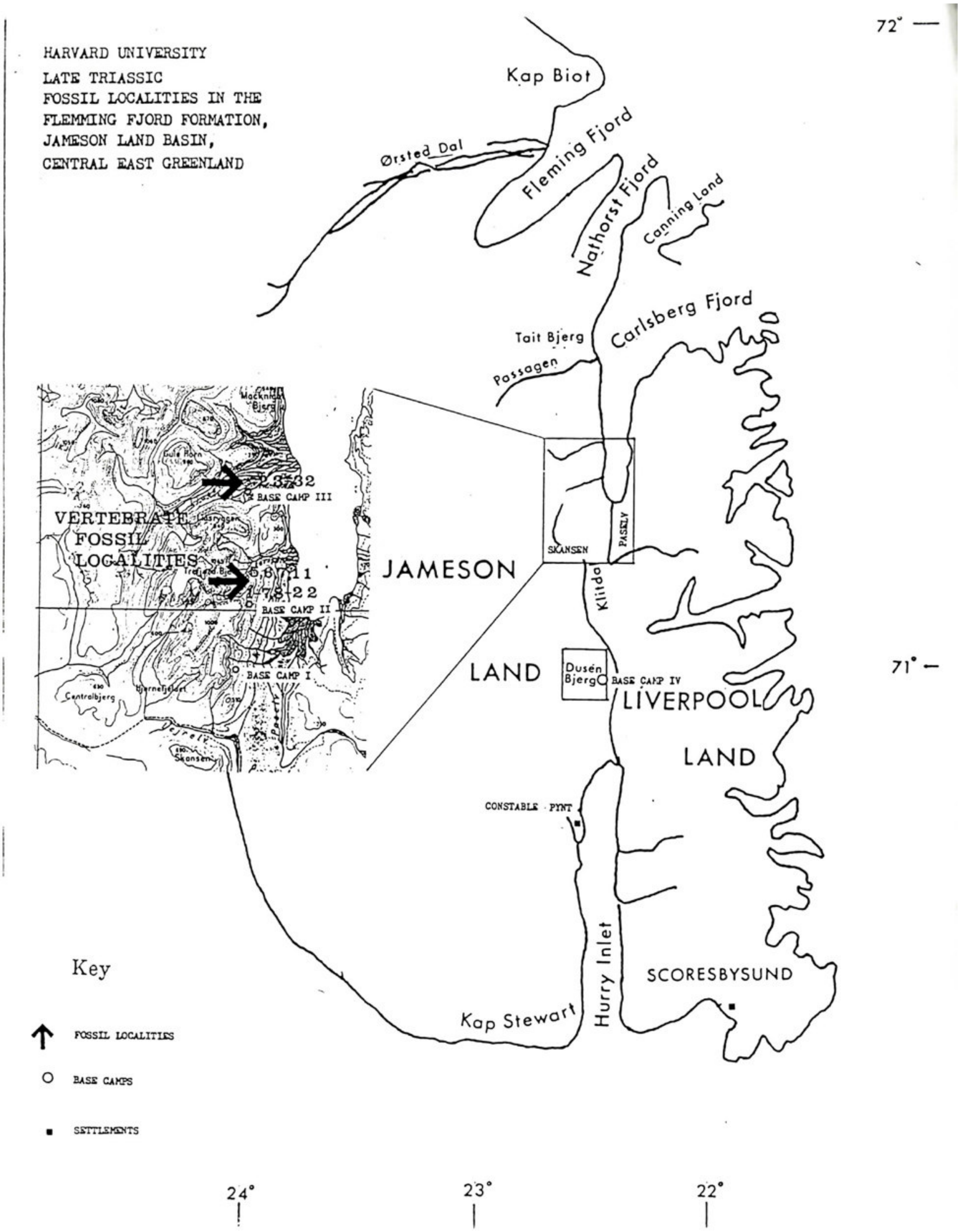
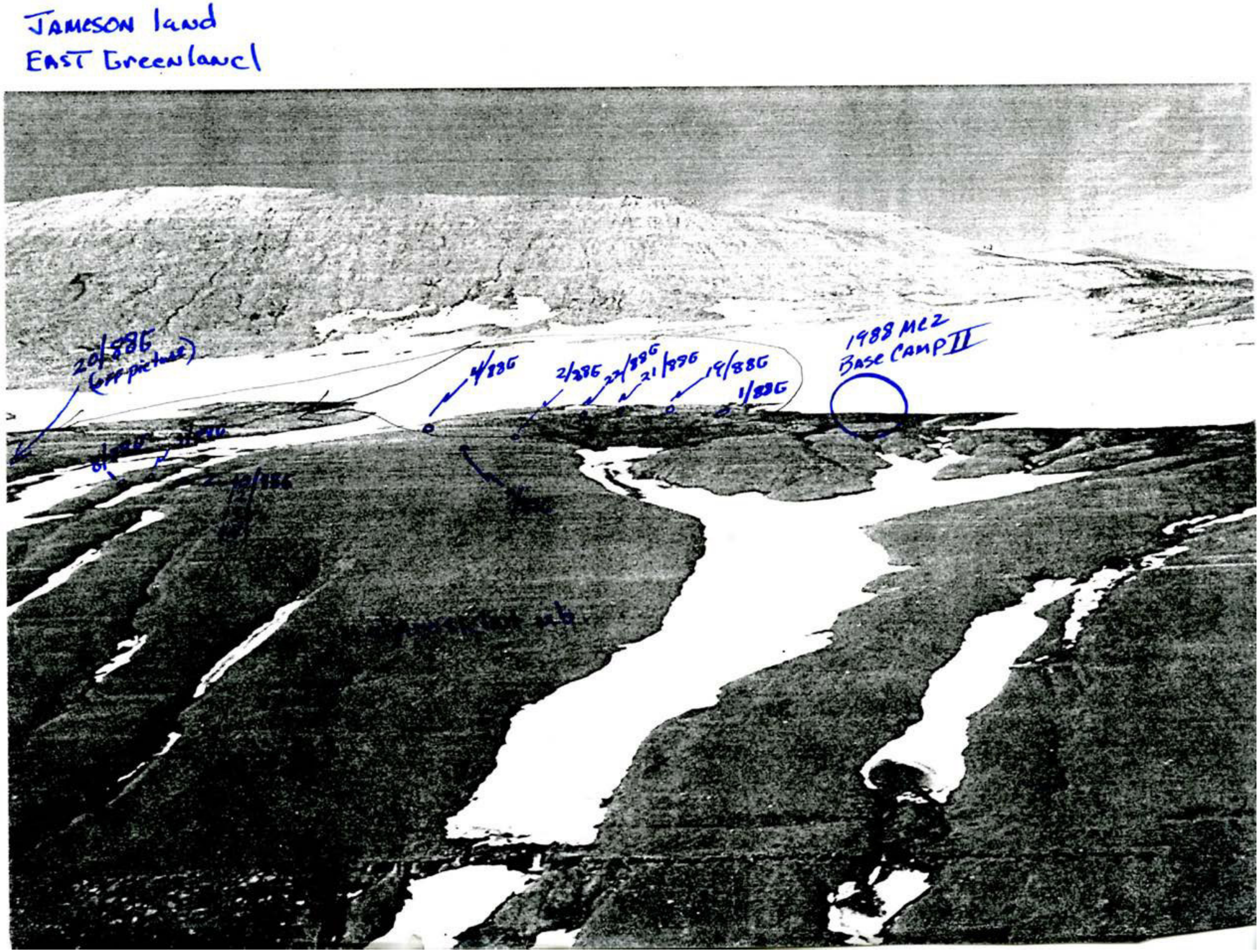
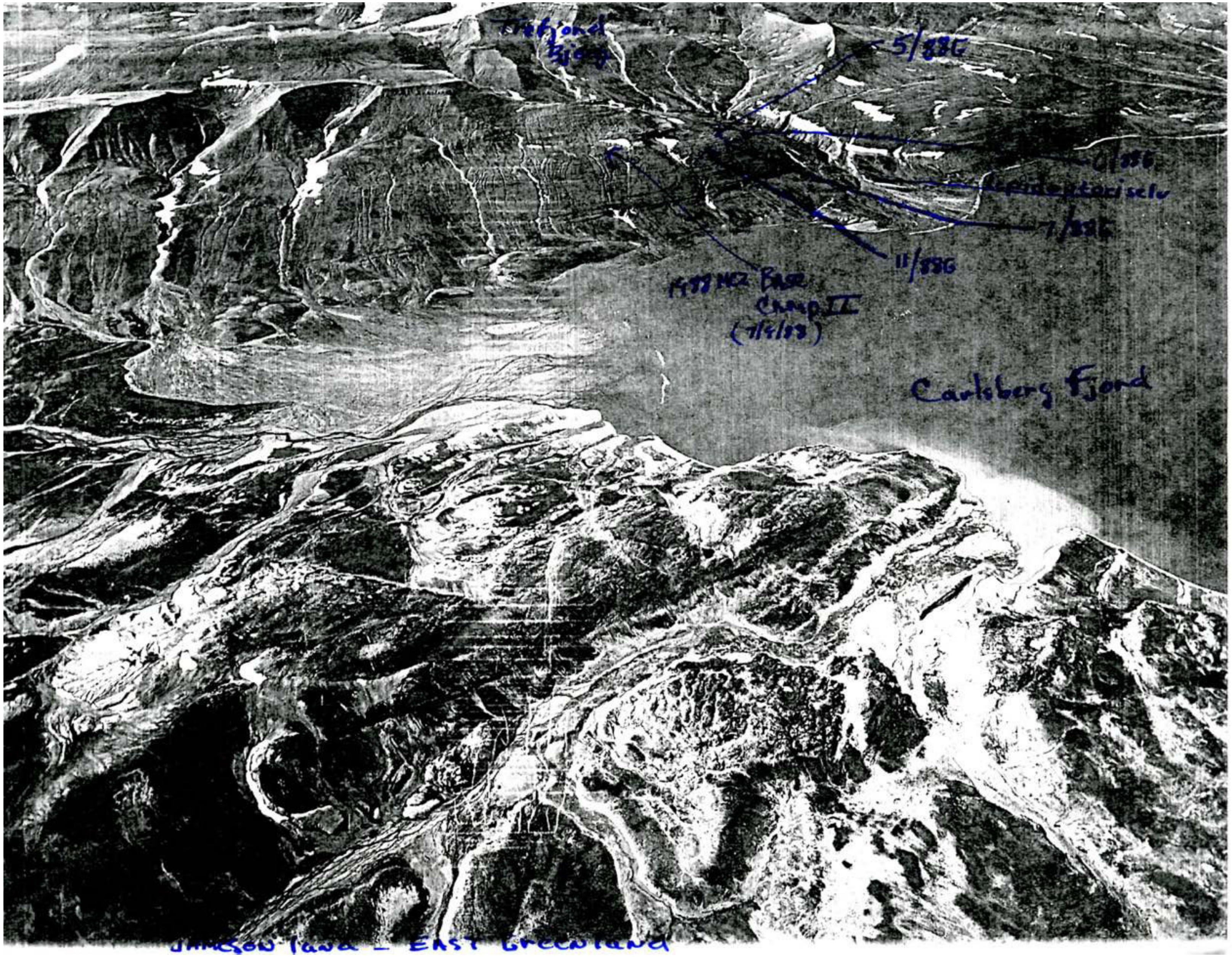
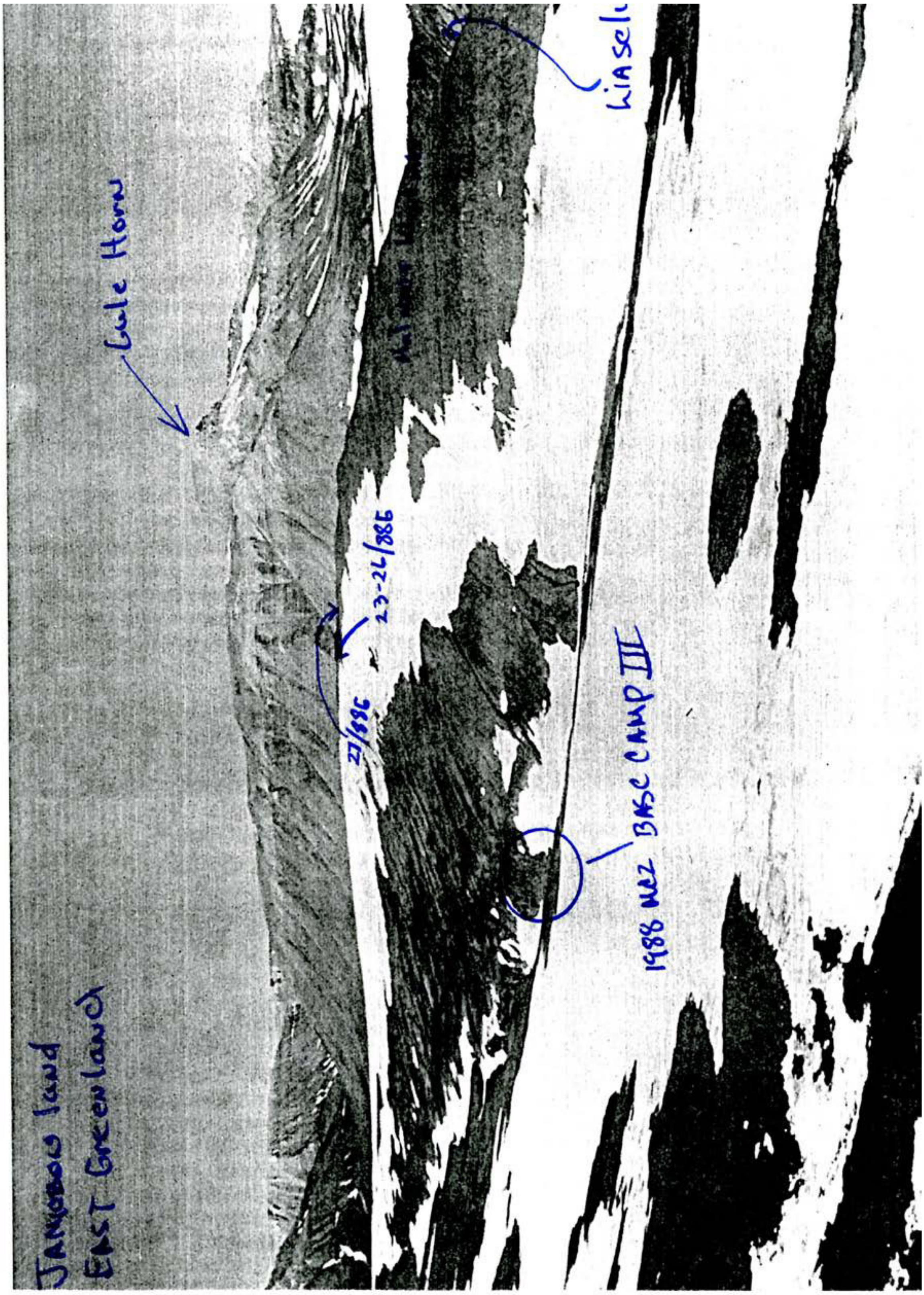

HARVARD UNIVERSITY
LATE TRIASSIC
FOSSIL LOCALITIES IN THE
FLEMMING FJORD FORMATION,
JAMESON LAND BASIN,
CENTRAL EAST GREENLAND
72°
Kap Biot
Ørsted Dal
Fleming Fjord
Nathorst Fjord
Canning Land
Carlsberg Fjord
Tait Bjerg
Passagen
Mackni Bjerg
Gule Horn
VERTEBRATE
FOSSIL
LOCALITIES
32
BASE CAMP III
Lissryggen
Trefjeld Bjerg
5,6,7,11
22
BASE CAMP II
BASE CAMP I
Centralbjerg
Hjørnefjeldet
Vejrelv
Skansen
JAMESON
LAND
SKANSEN
PASSLY
Klitdal
Dusén Bjerg
BASE CAMP IV
71°
LIVERPOOL
LAND
CONSTABLE PYNT
Hurry Inlet
SCORESBYSUND
Kap Stewart
Key
FOSSIL LOCALITIES
BASE CAMPS
SETTLEMENTS
24°
23°
22°

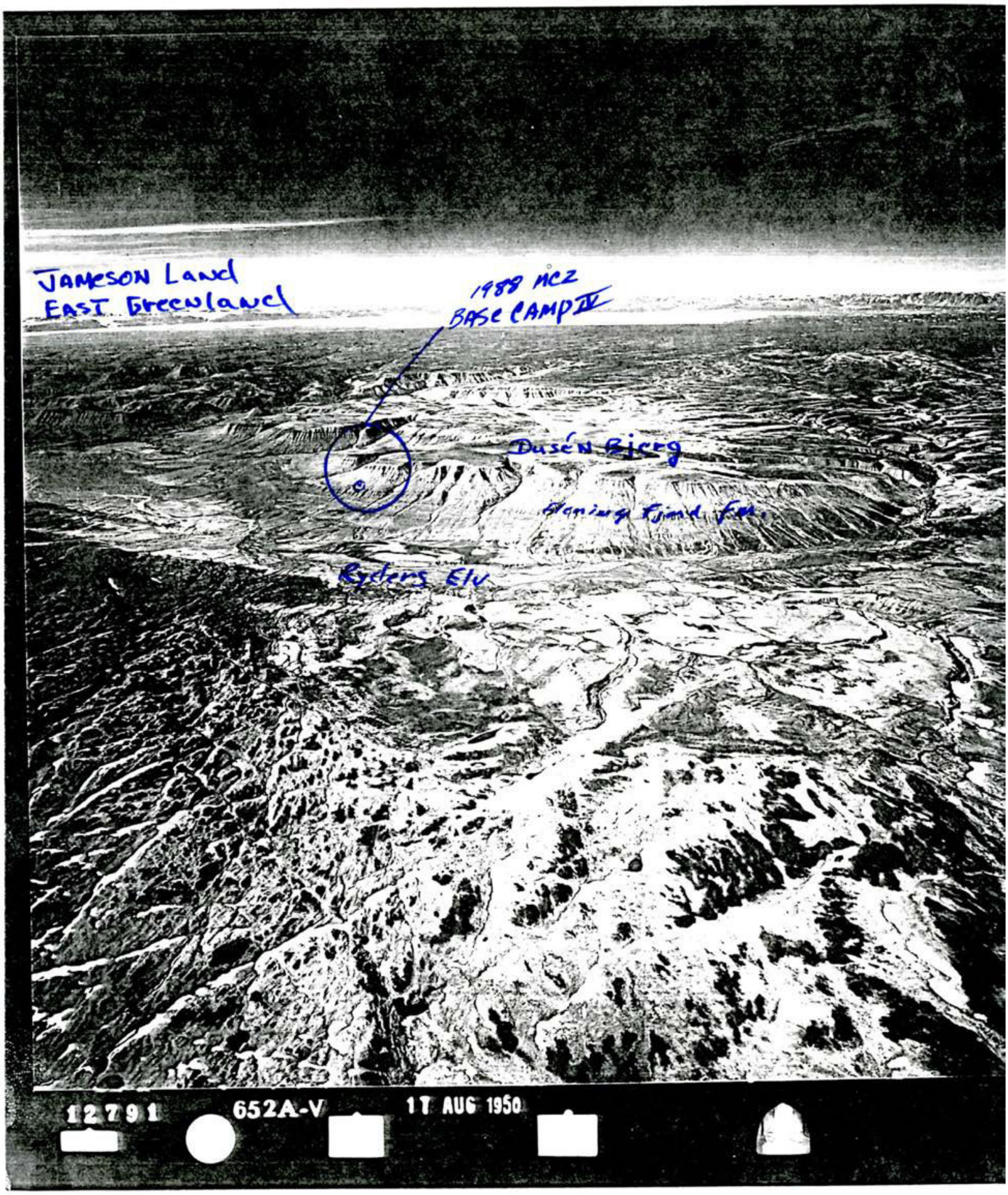

HARVARD UNIVERSITY
LATE TRIASSIC
FOSSIL LOCALITIES IN THE
FLEMMING FJORD FORMATION,
JAMESON LAND BASIN,
CENTRAL EAST GREENLAND
72°
Kap Biot
Ørsted Dal
Fleming Fjord
Nathorst Fjord
Canning Land
Carlsberg Fjord
Tait Bjerg
Passagen
Macknight Bjerg
Gule Horn
VERTEBRATE
FOSSIL
LOCALITIES
2,3,32
BASE CAMP III
Trefjeld Bjerg
5,6,11
1,7,8,22
BASE CAMP II
BASE CAMP I
Centralbjerg
Bjerneljeldet
Skansen
SKANSEN
PASKLY
JAMESON
LAND
Klitdal
Dusén Bjerg
BASE CAMP IV
71°
LIVERPOOL
LAND
CONSTABLE PYNT
Hurry Inlet
SCORESBYSUND
Kap Stewart
Key
FOSSIL LOCALITIES
BASE CAMPS
SETTLEMENTS
24°
23°
22°


1988 MCZ
Base
Camp I
Hjørnefjeldet
Lejrelv
Skansen
653A-V


JAMESON land
EAST Greenland
20/88G
(off picture)
4/88G
2/88G
27/88G
21/88G
19/88G
1/88G
1988 MCZ
Base CAMP II


Trefjord Bjerg
5/88G
6/88G
Lepidopteriselv
7/88G
11/88G
1988 MCZ Base Camp II (7/4/88)
Carlsberg Fjord
Jameson Land – East Greenland


Jameson land
EAST Greenland
Lule Horn
23-26/88B
27/88C
1988 NEZ BASE CAMP III
Liasel


Jameson Land
East Greenland
1989 MCZ
Base Camp IV
Dusén Bjerg
Fleming Fjord Fm.
Ryders Elv
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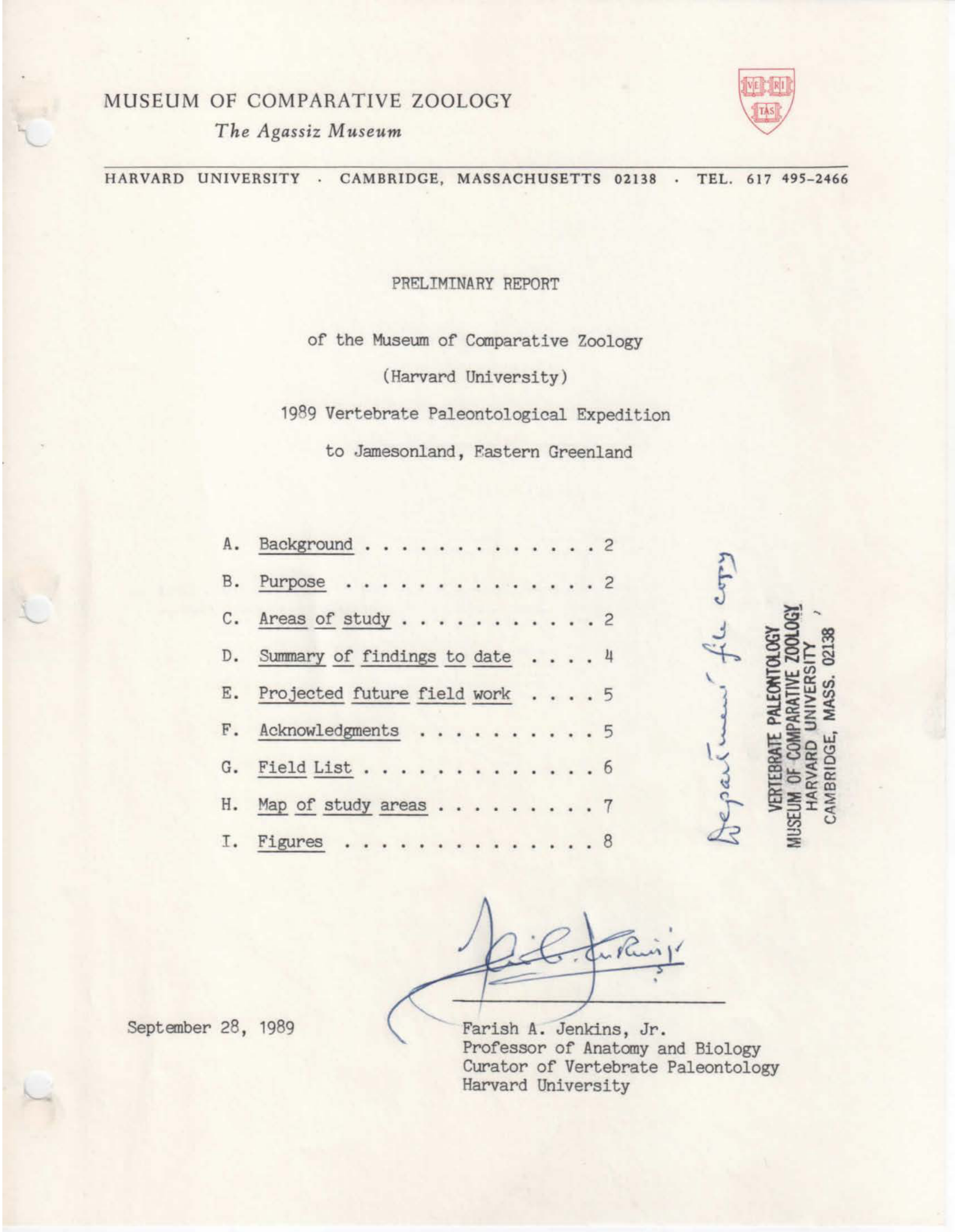
A6 – Field report 1989 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1989 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenlan



MUSEUM OF COMPARATIVE ZOOLOGY
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VERTEBRATE PALEONTOLOGY
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY
CAMBRIDGE, MASS. 02138

September 28, 1989

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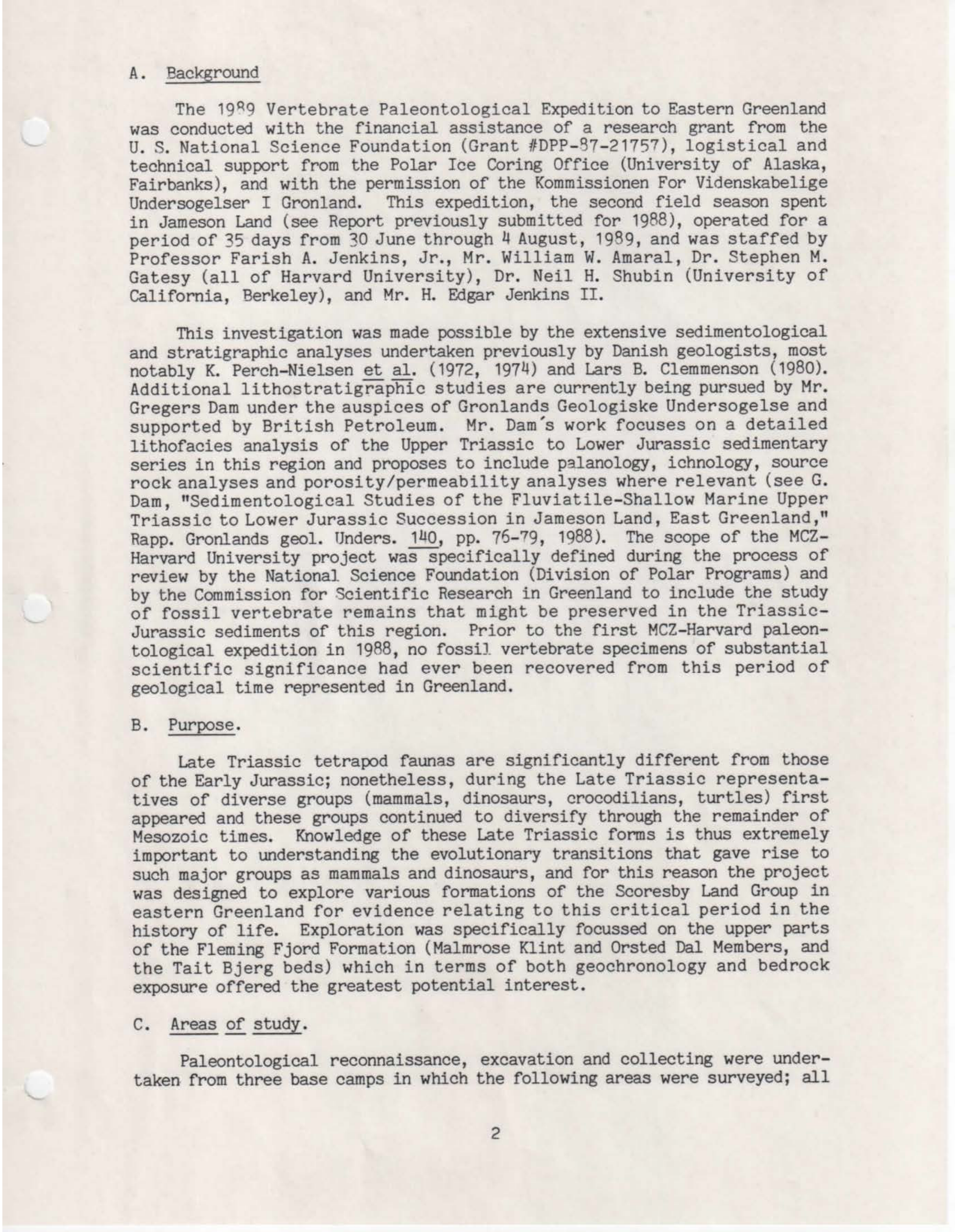


A. Background

The 1989 Vertebrate Paleontological Expedition to Eastern Greenland was conducted with the financial assistance of a research grant from the U. S. National Science Foundation (Grant #DPP-87-21757), logistical and technical support from the Polar Ice Coring Office (University of Alaska, Fairbanks), and with the permission of the Kommissionen For Videnskabelige Undersogelser I Gronland. This expedition, the second field season spent in Jameson Land (see Report previously submitted for 1988), operated for a period of 35 days from 30 June through 4 August, 1989, and was staffed by Professor Farish A. Jenkins, Jr., Mr. William W. Amaral, Dr. Stephen M. Gatesy (all of Harvard University), Dr. Neil H. Shubin (University of California, Berkeley), and Mr. H. Edgar Jenkins II.

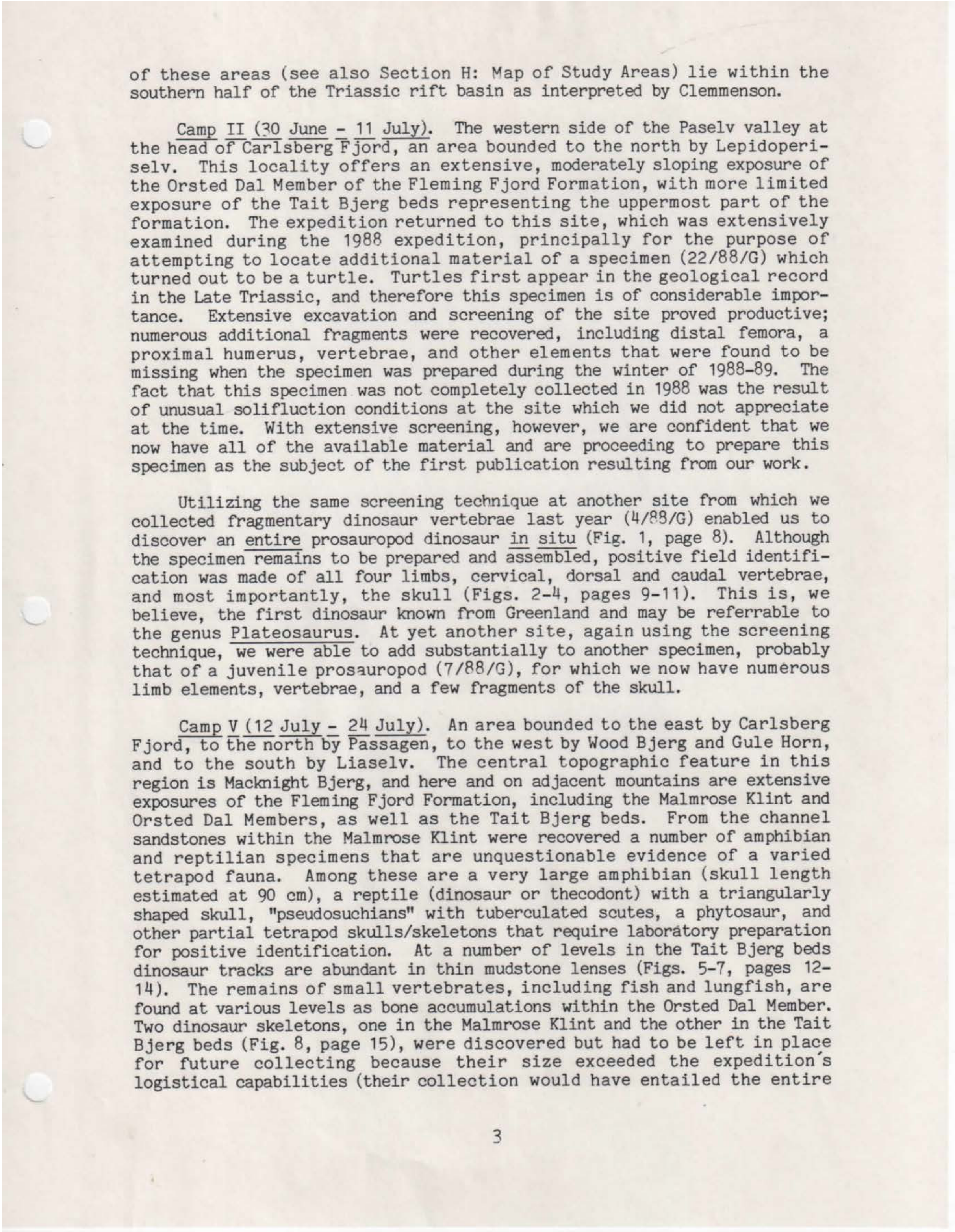
This investigation was made possible by the extensive sedimentological and stratigraphic analyses undertaken previously by Danish geologists, most notably K. Perch-Nielsen *et al.* (1972, 1974) and Lars B. Clemmenson (1980). Additional lithostratigraphic studies are currently being pursued by Mr. Gregers Dam under the auspices of Gronlands Geologiske Undersogelse and supported by British Petroleum. Mr. Dam's work focuses on a detailed lithofacies analysis of the Upper Triassic to Lower Jurassic sedimentary series in this region and proposes to include palanology, ichnology, source rock analyses and porosity/permeability analyses where relevant (see G. Dam, "Sedimentological Studies of the Fluviatile-Shallow Marine Upper Triassic to Lower Jurassic Succession in Jameson Land, East Greenland," Rapp. Gronlands geol. Unders. *140*, pp. 76-79, 1988). The scope of the MCZ-Harvard University project was specifically defined during the process of review by the National Science Foundation (Division of Polar Programs) and by the Commission for Scientific Research in Greenland to include the study of fossil vertebrate remains that might be preserved in the Triassic-Jurassic sediments of this region. Prior to the first MCZ-Harvard paleontological expedition in 1988, no fossil vertebrate specimens of substantial scientific significance had ever been recovered from this period of geological time represented in Greenland.

B. Purpose.

Late Triassic tetrapod faunas are significantly different from those of the Early Jurassic; nonetheless, during the Late Triassic representatives of diverse groups (mammals, dinosaurs, crocodilians, turtles) first appeared and these groups continued to diversify through the remainder of Mesozoic times. Knowledge of these Late Triassic forms is thus extremely important to understanding the evolutionary transitions that gave rise to such major groups as mammals and dinosaurs, and for this reason the project was designed to explore various formations of the Scoresby Land Group in eastern Greenland for evidence relating to this critical period in the history of life. Exploration was specifically focussed on the upper parts of the Fleming Fjord Formation (Malmrose Klint and Orsted Dal Members, and the Tait Bjerg beds) which in terms of both geochronology and bedrock exposure offered the greatest potential interest.

C. Areas of study.

Paleontological reconnaissance, excavation and collecting were undertaken from three base camps in which the following areas were surveyed; all



of these areas (see also Section H: Map of Study Areas) lie within the southern half of the Triassic rift basin as interpreted by Clemmenson.

Camp II (30 June - 11 July). The western side of the Paselv valley at the head of Carlsberg Fjord, an area bounded to the north by Lepidoperiselv. This locality offers an extensive, moderately sloping exposure of the Orsted Dal Member of the Fleming Fjord Formation, with more limited exposure of the Tait Bjerg beds representing the uppermost part of the formation. The expedition returned to this site, which was extensively examined during the 1988 expedition, principally for the purpose of attempting to locate additional material of a specimen (22/88/G) which turned out to be a turtle. Turtles first appear in the geological record in the Late Triassic, and therefore this specimen is of considerable importance. Extensive excavation and screening of the site proved productive; numerous additional fragments were recovered, including distal femora, a proximal humerus, vertebrae, and other elements that were found to be missing when the specimen was prepared during the winter of 1988-89. The fact that this specimen was not completely collected in 1988 was the result of unusual solifluction conditions at the site which we did not appreciate at the time. With extensive screening, however, we are confident that we now have all of the available material and are proceeding to prepare this specimen as the subject of the first publication resulting from our work.

Utilizing the same screening technique at another site from which we collected fragmentary dinosaur vertebrae last year (4/88/G) enabled us to discover an entire prosauropod dinosaur in situ (Fig. 1, page 8). Although the specimen remains to be prepared and assembled, positive field identification was made of all four limbs, cervical, dorsal and caudal vertebrae, and most importantly, the skull (Figs. 2-4, pages 9-11). This is, we believe, the first dinosaur known from Greenland and may be referrable to the genus Plateosaurus. At yet another site, again using the screening technique, we were able to add substantially to another specimen, probably that of a juvenile prosauropod (7/88/G), for which we now have numerous limb elements, vertebrae, and a few fragments of the skull.

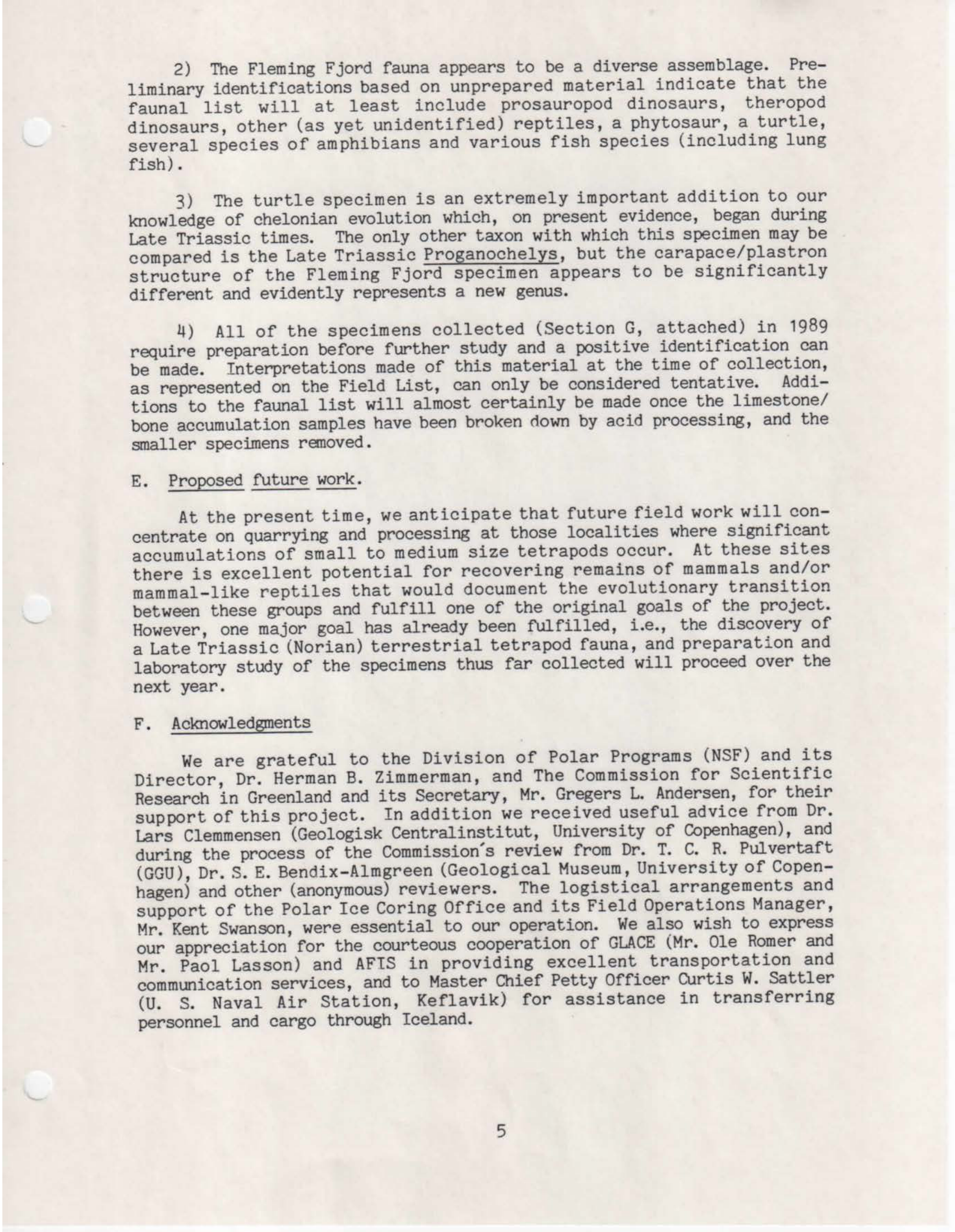
Camp V (12 July - 24 July). An area bounded to the east by Carlsberg Fjord, to the north by Passagen, to the west by Wood Bjerg and Gule Horn, and to the south by Liaselv. The central topographic feature in this region is Macknight Bjerg, and here and on adjacent mountains are extensive exposures of the Fleming Fjord Formation, including the Malmrose Klint and Orsted Dal Members, as well as the Tait Bjerg beds. From the channel sandstones within the Malmrose Klint were recovered a number of amphibian and reptilian specimens that are unquestionable evidence of a varied tetrapod fauna. Among these are a very large amphibian (skull length estimated at 90 cm), a reptile (dinosaur or thecodont) with a triangularly shaped skull, "pseudosuchians" with tuberculated scutes, a phytosaur, and other partial tetrapod skulls/skeletons that require laboratory preparation for positive identification. At a number of levels in the Tait Bjerg beds dinosaur tracks are abundant in thin mudstone lenses (Figs. 5-7, pages 12-14). The remains of small vertebrates, including fish and lungfish, are found at various levels as bone accumulations within the Orsted Dal Member. Two dinosaur skeletons, one in the Malmrose Klint and the other in the Tait Bjerg beds (Fig. 8, page 15), were discovered but had to be left in place for future collecting because their size exceeded the expedition´s logistical capabilities (their collection would have entailed the entire expeditionary effort for the rest of the season, and the weight of the specimens would have exceeded the planned allowances for shipment to CONUS). However, both specimens represent excellent potential for future work.

The most important discovery in the Camp V area is a fine-grained sandstone lense some 30 cm in thickness that apparently represents unusual preservational conditions. Within the lense are preserved innumerable tetrapod bones in good condition and exhibiting very little evidence of transport. Unlike other "bone beds" that may be found locally throughout the upper part of the Fleming Fjord Formation (which consist mostly of fish bones and scales that have been extensively transported), this site offers the possibility of sampling the entire local fauna of small to medium size tetrapods. It is at this locality, as well as others like it that were found subsequently elsewhere, that mammals and other paleontologically rare but significant forms may be expected to be found. Preliminary quarrying at the site produced complete bones of various amphibians and reptiles, including jaws that ranged in size from 2 to 7 cm in length (Fig. 9, page 16). Inasmuch as this lense is highly indurated, and bones could not be safely removed by conventional quarrying techniques, samples of the locality were taken (G/12/89) for laboratory examination and specifically for processing with acetic or formic acid to determine the most suitable technique for recovering specimens without any mechanical damage. The unusual abundance of bone at this locality, together with the broad representation of different elements of the fauna, represents our potentially most important discovery to date.

Camp VI (25 July - 4 August). An area encompassing the entirety of Tait Bjerg, bounded by Passagen to the south, Buch Bjerg to the north, and Carlsberg Fjord to the east. This area likewise provided excellent exposures of the Malmrose Klint and Orsted Dal Members, as well as the type locality for the Tait Bjerg beds at the summit of the mountain. Sandstone channels in the Malmrose Klint yielded various partial skeletons and skulls of amphibians and reptiles; dinosaur tracks again occur in the Orsted Dal Member as well as in the Tait Bjerg beds. Another large dinosaur, of uncertain taxonomic affinity, was located within the Malmrose Klint but, for the same logistical reasons that prevented collecting certain specimens in the Camp V area, it was marked for excavation in the future. Two additional sites of abundant tetrapod bone concentration were located and samples taken for acid preparation and laboratory examination. We thus have three localities at different stratigraphic levels within the upper part of the Fleming Fjord Formation that have the potential to provide an excellent compositional sample of the Late Triassic, small to medium size tetrapod fauna.

D. Summary of findings to date.

1) A diverse fossil vertebrate fauna of Late Triassic age has been discovered in the Fleming Fjord Formation in eastern Greenland. Fossil localities occur throughout the upper Fleming Fjord, namely in the Malmrose Klint and Orsted Dal Members, including the uppermost Tait Bjerg beds. Vertebrate remains are associated with a variety of lacustrine, fluviatile and subaerial environments; terrestrial tetrapods occur predominantly in red channel sandstones within the Malmrose Klint Member and also in local but very abundant concentrations within limestone lenses.



2) The Fleming Fjord fauna appears to be a diverse assemblage. Preliminary identifications based on unprepared material indicate that the faunal list will at least include prosauropod dinosaurs, theropod dinosaurs, other (as yet unidentified) reptiles, a phytosaur, a turtle, several species of amphibians and various fish species (including lung fish).

3) The turtle specimen is an extremely important addition to our knowledge of chelonian evolution which, on present evidence, began during Late Triassic times. The only other taxon with which this specimen may be compared is the Late Triassic Proganochelys, but the carapace/plastron structure of the Fleming Fjord specimen appears to be significantly different and evidently represents a new genus.

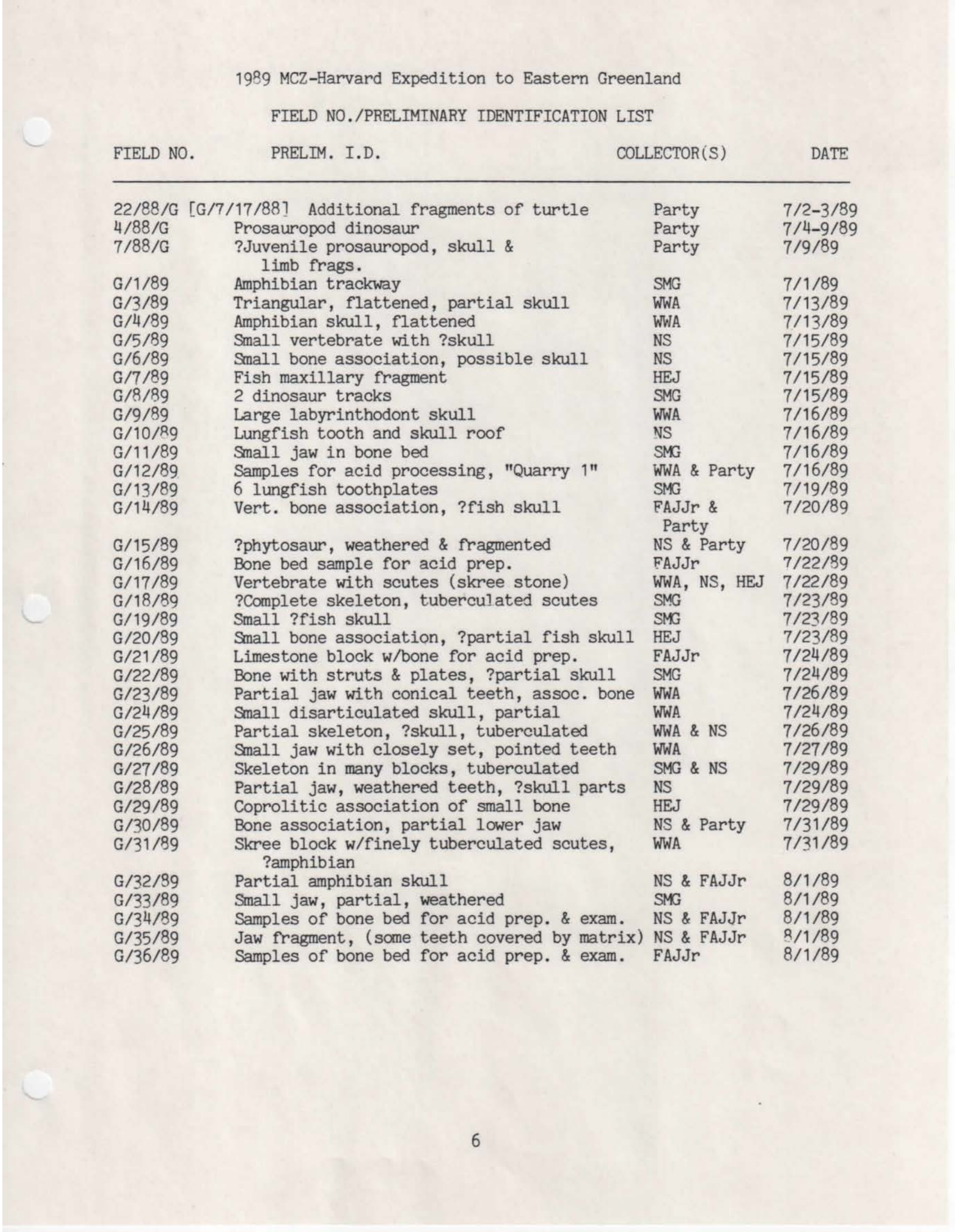
4) All of the specimens collected (Section G, attached) in 1989 require preparation before further study and a positive identification can be made. Interpretations made of this material at the time of collection, as represented on the Field List, can only be considered tentative. Additions to the faunal list will almost certainly be made once the limestone/bone accumulation samples have been broken down by acid processing, and the smaller specimens removed.

E. Proposed future work.

At the present time, we anticipate that future field work will concentrate on quarrying and processing at those localities where significant accumulations of small to medium size tetrapods occur. At these sites there is excellent potential for recovering remains of mammals and/or mammal-like reptiles that would document the evolutionary transition between these groups and fulfill one of the original goals of the project. However, one major goal has already been fulfilled, i.e., the discovery of a Late Triassic (Norian) terrestrial tetrapod fauna, and preparation and laboratory study of the specimens thus far collected will proceed over the next year.

F. Acknowledgments

We are grateful to the Division of Polar Programs (NSF) and its Director, Dr. Herman B. Zimmerman, and The Commission for Scientific Research in Greenland and its Secretary, Mr. Gregers L. Andersen, for their support of this project. In addition we received useful advice from Dr. Lars Clemmensen (Geologisk Centralinstitut, University of Copenhagen), and during the process of the Commission's review from Dr. T. C. R. Pulvertaft (GGU), Dr. S. E. Bendix-Almgreen (Geological Museum, University of Copenhagen) and other (anonymous) reviewers. The logistical arrangements and support of the Polar Ice Coring Office and its Field Operations Manager, Mr. Kent Swanson, were essential to our operation. We also wish to express our appreciation for the courteous cooperation of GLACE (Mr. Ole Romer and Mr. Paol Lasson) and AFIS in providing excellent transportation and communication services, and to Master Chief Petty Officer Curtis W. Sattler (U. S. Naval Air Station, Keflavik) for assistance in transferring personnel and cargo through Iceland.

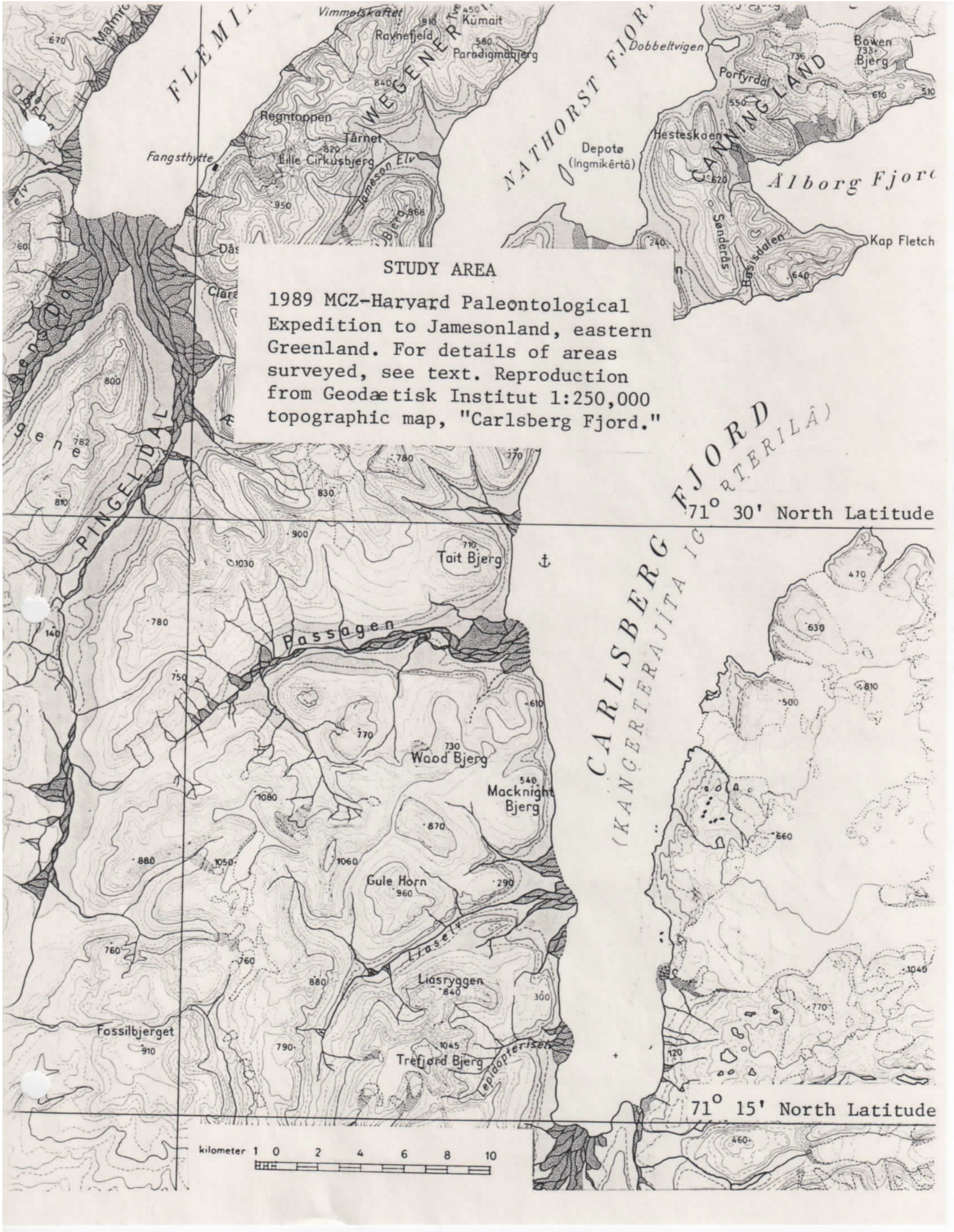


1989 MCZ-Harvard Expedition to Eastern Greenland

FIELD NO./PRELIMINARY IDENTIFICATION LIST

FIELD NO.	PRELIM. I.D.	COLLECTOR(S)	DATE
22/88/G [G/7/17/88]	Additional fragments of turtle	Party	7/2-3/89
4/88/G	Prosauropod dinosaur	Party	7/4-9/89
7/88/G	?Juvenile prosauropod, skull & limb frags.	Party	7/9/89
G/1/89	Amphibian trackway	SMG	7/1/89
G/3/89	Triangular, flattened, partial skull	WWA	7/13/89
G/4/89	Amphibian skull, flattened	WWA	7/13/89
G/5/89	Small vertebrate with ?skull	NS	7/15/89
G/6/89	Small bone association, possible skull	NS	7/15/89
G/7/89	Fish maxillary fragment	HEJ	7/15/89
G/8/89	2 dinosaur tracks	SMG	7/15/89
G/9/89	Large labyrinthodont skull	WWA	7/16/89
G/10/89	Lungfish tooth and skull roof	NS	7/16/89
G/11/89	Small jaw in bone bed	SMG	7/16/89
G/12/89	Samples for acid processing, "Quarry 1"	WWA & Party	7/16/89
G/13/89	6 lungfish toothplates	SMG	7/19/89
G/14/89	Vert. bone association, ?fish skull	FAJJr & Party	7/20/89
G/15/89	?phytosaur, weathered & fragmented	NS & Party	7/20/89
G/16/89	Bone bed sample for acid prep.	FAJJr	7/22/89
G/17/89	Vertebrate with scutes (skree stone)	WWA, NS, HEJ	7/22/89
G/18/89	?Complete skeleton, tuberculated scutes	SMG	7/23/89
G/19/89	Small ?fish skull	SMG	7/23/89
G/20/89	Small bone association, ?partial fish skull	HEJ	7/23/89
G/21/89	Limestone block w/bone for acid prep.	FAJJr	7/24/89
G/22/89	Bone with struts & plates, ?partial skull	SMG	7/24/89
G/23/89	Partial jaw with conical teeth, assoc. bone	WWA	7/26/89
G/24/89	Small disarticulated skull, partial	WWA	7/24/89
G/25/89	Partial skeleton, ?skull, tuberculated	WWA & NS	7/26/89
G/26/89	Small jaw with closely set, pointed teeth	WWA	7/27/89
G/27/89	Skeleton in many blocks, tuberculated	SMG & NS	7/29/89
G/28/89	Partial jaw, weathered teeth, ?skull parts	NS	7/29/89
G/29/89	Coprolitic association of small bone	HEJ	7/29/89
G/30/89	Bone association, partial lower jaw	NS & Party	7/31/89
G/31/89	Skree block w/finely tuberculated scutes, ?amphibian	WWA	7/31/89
G/32/89	Partial amphibian skull	NS & FAJJr	8/1/89
G/33/89	Small jaw, partial, weathered	SMG	8/1/89
G/34/89	Samples of bone bed for acid prep. & exam.	NS & FAJJr	8/1/89
G/35/89	Jaw fragment, (some teeth covered by matrix)	NS & FAJJr	8/1/89
G/36/89	Samples of bone bed for acid prep. & exam.	FAJJr	8/1/89

6



STUDY AREA

1989 MCZ-Harvard Paleontological Expedition to Jamesonland, eastern Greenland. For details of areas surveyed, see text. Reproduction from Geodætisk Institut 1:250,000 topographic map, "Carlsberg Fjord."

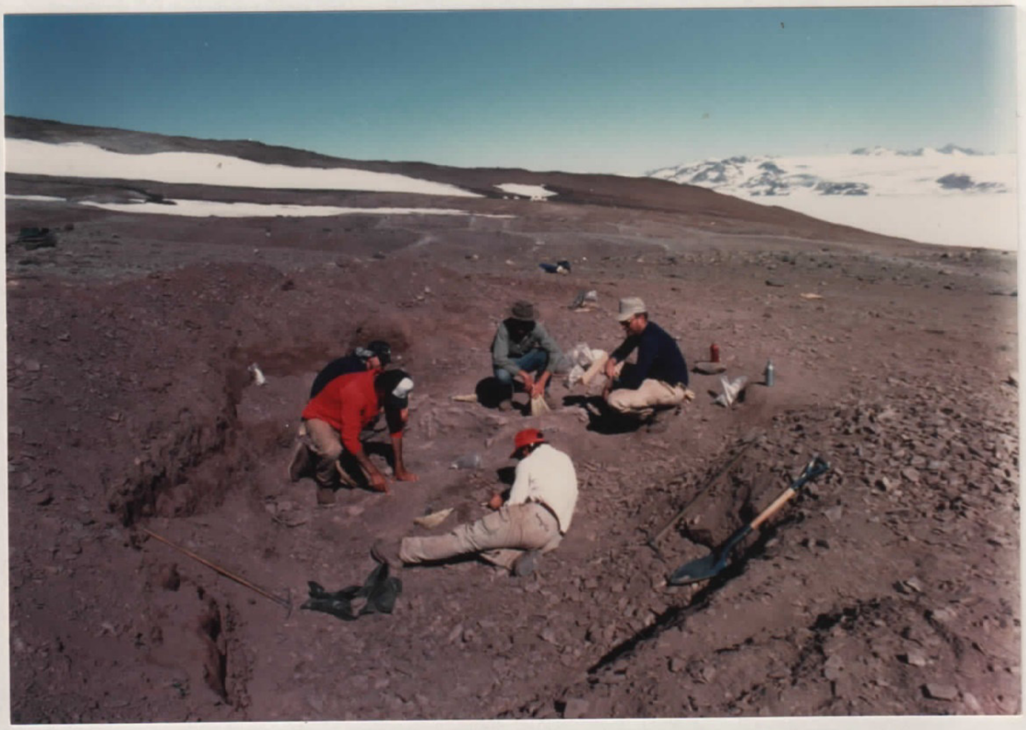


Fig. 1 Prosauropod dinosaur quarry, Camp II (small cluster of white tents) in background. Approximately 22 cubic yards of sediment were excavated to expose the specimen.

Fig. 2 Prosauropod dinosaur quarry. Dr. Neil Shubin is in the process of removing the left manus, beneath which lay the skull. Various elements of the pelvis lie in the foreground.

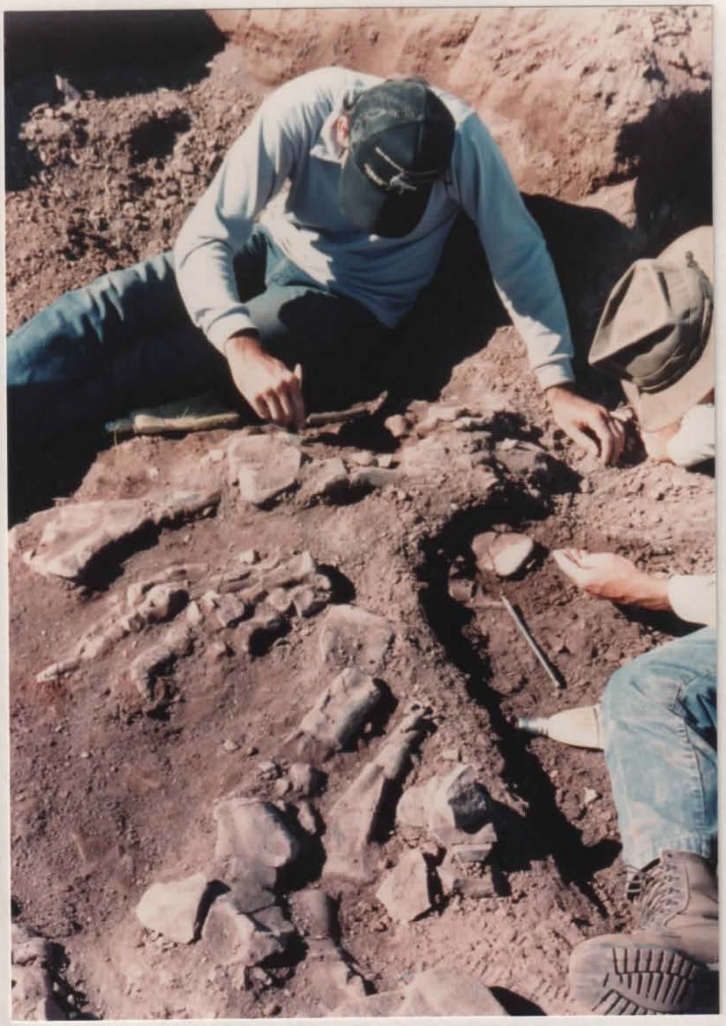


Fig. 3 Prosauropod dinosaur quarry. Dr. Gatesy (top) and Mr. Jenkins (right) are cleaning and removing bones of the pelvis. The right hindfoot is seen at center left (cf. Fig. 4, page 11).

Fig. 4 Prosauropod dinosaur quarry. Complete right hindfoot *in situ*. The instrument at the bottom is 4 inches (10.2 cm) long.

Fig. 5 Footprint of a theropod dinosaur, approximately 8 inches (20 cm) in length. Footprints of this type were the most common.

Fig. 6 Trackways of theropod dinosaurs. One set of footprints crosses from left to right; another trail leads from the bottom of the figure off into the horizon.

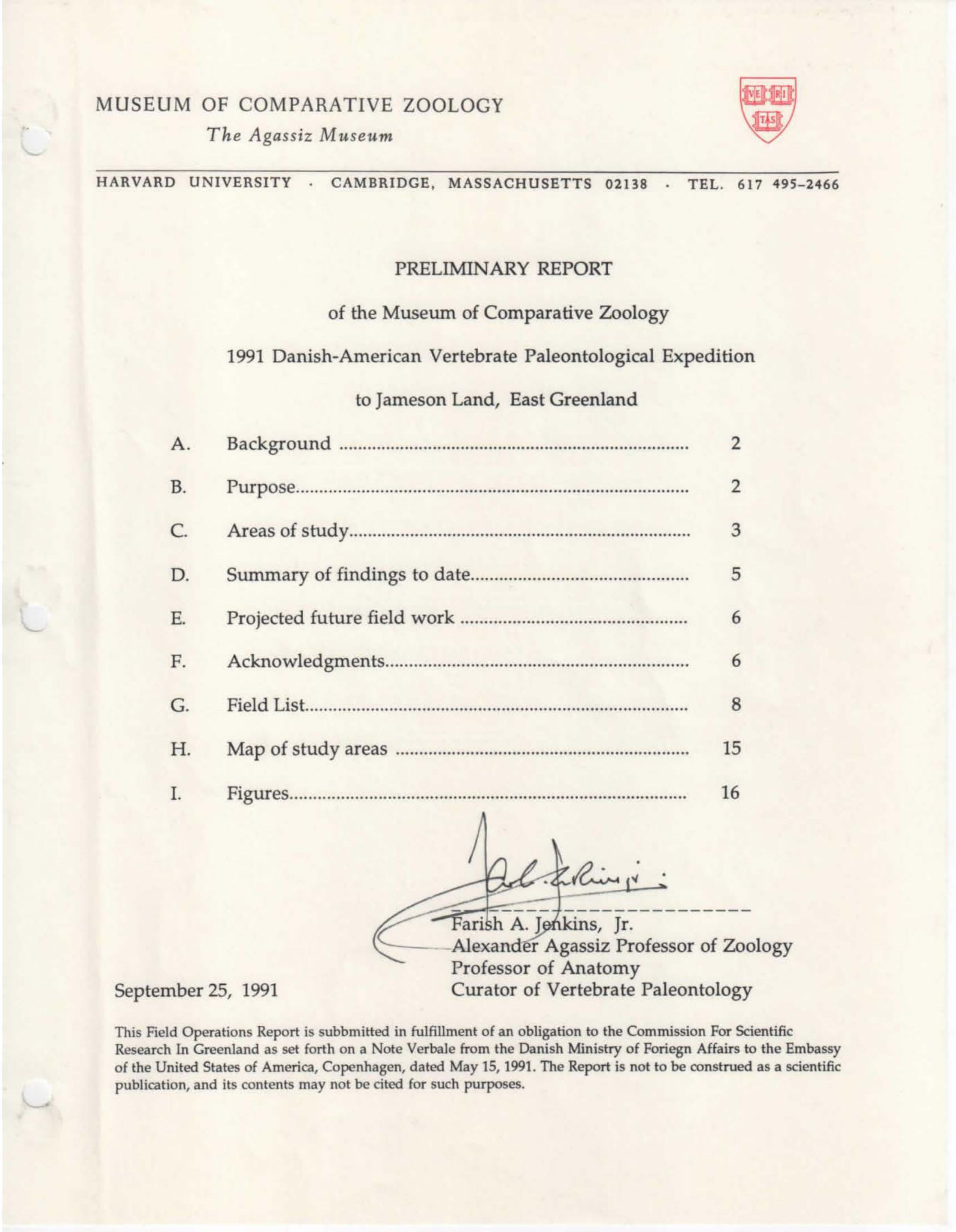
Fig. 7 Footprints of large dinosaur, probably prosauropod. These tracks are approximately 12 inches (30 cm) in width.

Fig. 8 Dinosaur bone, representing a specimen in situ, being exposed as the surrounding sediment is weathered and eroded.

Fig. 9 Samples from "Quarry 1" site showing tetrapod bone concentration, including jaws and a skull.

A7 – Field report 1991 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1991 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



MUSEUM OF COMPARATIVE ZOOLOGY
The Agassiz Museum

HARVARD UNIVERSITY · CAMBRIDGE, MASSACHUSETTS 02138 · TEL. 617 495-2466

PRELIMINARY REPORT

of the Museum of Comparative Zoology

1991 Danish-American Vertebrate Paleontological Expedition

to Jameson Land, East Greenland

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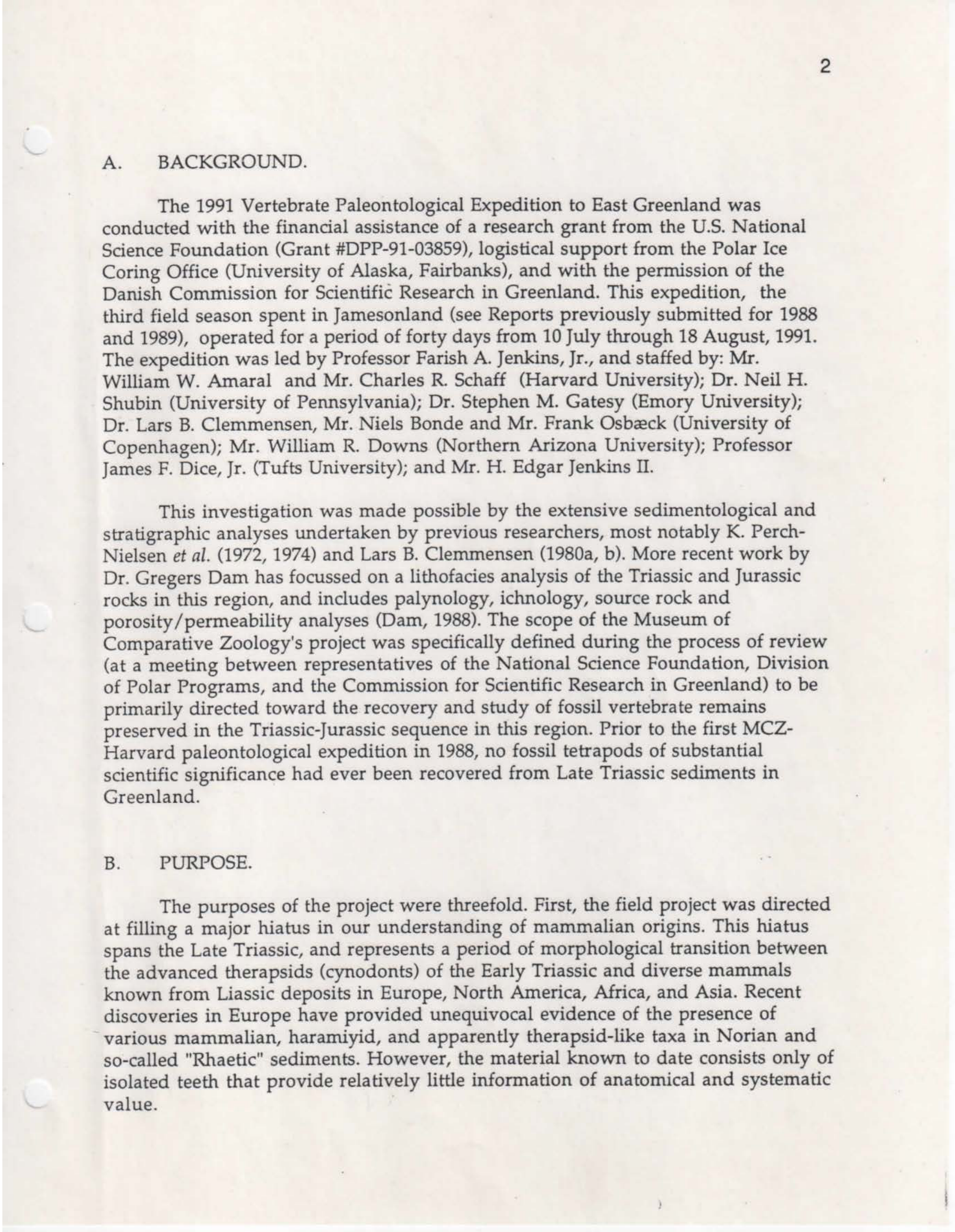
I. Figures 16

Farish A. Jenkins, Jr.
Alexander Agassiz Professor of Zoology
Professor of Anatomy
Curator of Vertebrate Paleontology

September 25, 1991

This Field Operations Report is subbmitted in fulfillment of an obligation to the Commission For Scientific Research In Greenland as set forth on a Note Verbale from the Danish Ministry of Foriegn Affairs to the Embassy of the United States of America, Copenhagen, dated May 15, 1991. The Report is not to be construed as a scientific publication, and its contents may not be cited for such purposes.



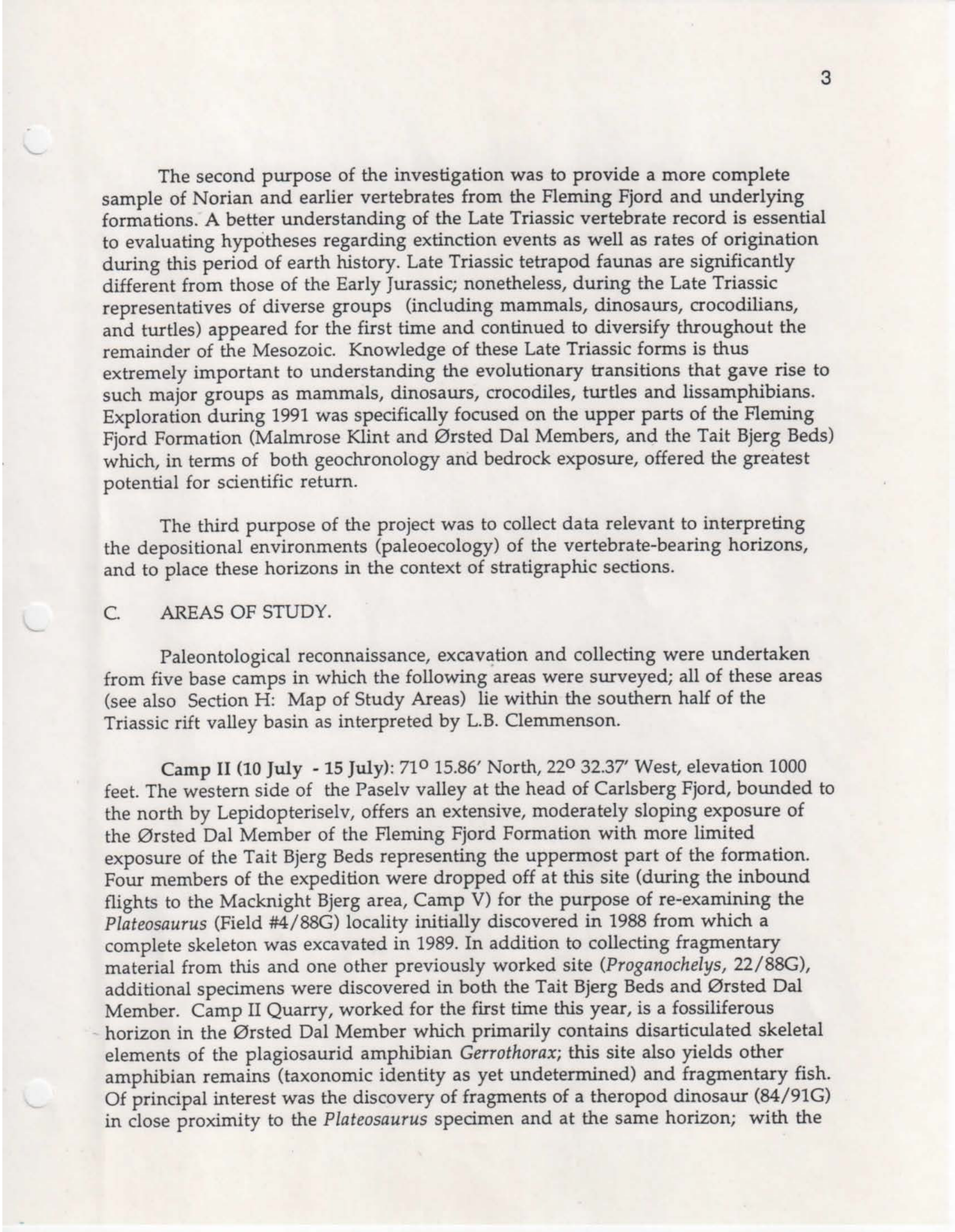
A. BACKGROUND.

The 1991 Vertebrate Paleontological Expedition to East Greenland was conducted with the financial assistance of a research grant from the U.S. National Science Foundation (Grant #DPP-91-03859), logistical support from the Polar Ice Coring Office (University of Alaska, Fairbanks), and with the permission of the Danish Commission for Scientific Research in Greenland. This expedition, the third field season spent in Jamesonland (see Reports previously submitted for 1988 and 1989), operated for a period of forty days from 10 July through 18 August, 1991. The expedition was led by Professor Farish A. Jenkins, Jr., and staffed by: Mr. William W. Amaral and Mr. Charles R. Schaff (Harvard University); Dr. Neil H. Shubin (University of Pennsylvania); Dr. Stephen M. Gatesy (Emory University); Dr. Lars B. Clemmensen, Mr. Niels Bonde and Mr. Frank Osbæck (University of Copenhagen); Mr. William R. Downs (Northern Arizona University); Professor James F. Dice, Jr. (Tufts University); and Mr. H. Edgar Jenkins II.

This investigation was made possible by the extensive sedimentological and stratigraphic analyses undertaken by previous researchers, most notably K. Perch-Nielsen *et al.* (1972, 1974) and Lars B. Clemmensen (1980a, b). More recent work by Dr. Gregers Dam has focussed on a lithofacies analysis of the Triassic and Jurassic rocks in this region, and includes palynology, ichnology, source rock and porosity/permeability analyses (Dam, 1988). The scope of the Museum of Comparative Zoology's project was specifically defined during the process of review (at a meeting between representatives of the National Science Foundation, Division of Polar Programs, and the Commission for Scientific Research in Greenland) to be primarily directed toward the recovery and study of fossil vertebrate remains preserved in the Triassic-Jurassic sequence in this region. Prior to the first MCZ-Harvard paleontological expedition in 1988, no fossil tetrapods of substantial scientific significance had ever been recovered from Late Triassic sediments in Greenland.

B. PURPOSE.

The purposes of the project were threefold. First, the field project was directed at filling a major hiatus in our understanding of mammalian origins. This hiatus spans the Late Triassic, and represents a period of morphological transition between the advanced therapsids (cynodonts) of the Early Triassic and diverse mammals known from Liassic deposits in Europe, North America, Africa, and Asia. Recent discoveries in Europe have provided unequivocal evidence of the presence of various mammalian, haramiyid, and apparently therapsid-like taxa in Norian and so-called "Rhaetic" sediments. However, the material known to date consists only of isolated teeth that provide relatively little information of anatomical and systematic value.



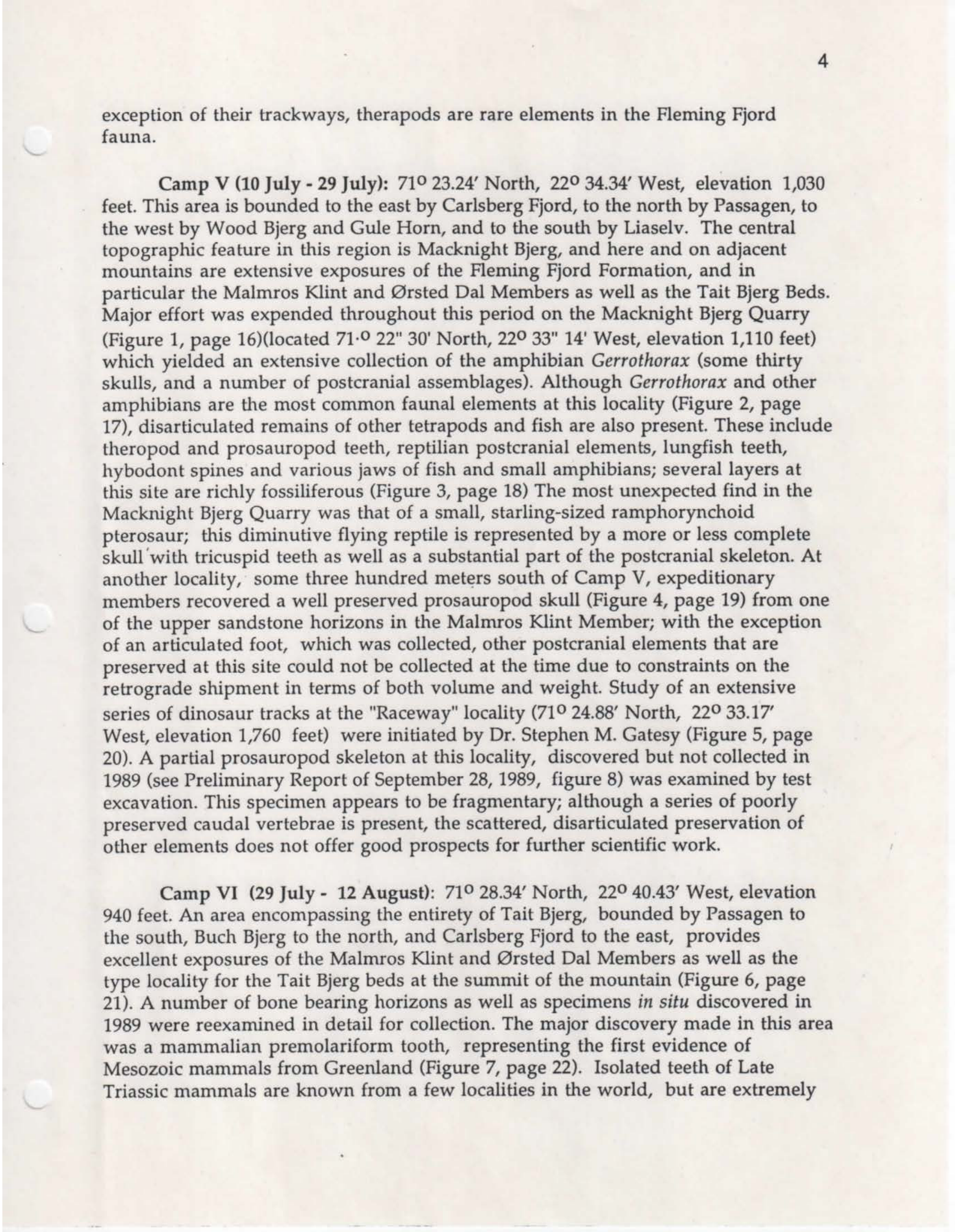
The second purpose of the investigation was to provide a more complete sample of Norian and earlier vertebrates from the Fleming Fjord and underlying formations. A better understanding of the Late Triassic vertebrate record is essential to evaluating hypotheses regarding extinction events as well as rates of origination during this period of earth history. Late Triassic tetrapod faunas are significantly different from those of the Early Jurassic; nonetheless, during the Late Triassic representatives of diverse groups (including mammals, dinosaurs, crocodilians, and turtles) appeared for the first time and continued to diversify throughout the remainder of the Mesozoic. Knowledge of these Late Triassic forms is thus extremely important to understanding the evolutionary transitions that gave rise to such major groups as mammals, dinosaurs, crocodiles, turtles and lissamphibians. Exploration during 1991 was specifically focused on the upper parts of the Fleming Fjord Formation (Malmrose Klint and Ørsted Dal Members, and the Tait Bjerg Beds) which, in terms of both geochronology and bedrock exposure, offered the greatest potential for scientific return.

The third purpose of the project was to collect data relevant to interpreting the depositional environments (paleoecology) of the vertebrate-bearing horizons, and to place these horizons in the context of stratigraphic sections.

C. AREAS OF STUDY.

Paleontological reconnaissance, excavation and collecting were undertaken from five base camps in which the following areas were surveyed; all of these areas (see also Section H: Map of Study Areas) lie within the southern half of the Triassic rift valley basin as interpreted by L.B. Clemmenson.

Camp II (10 July - 15 July): 71^{o} 15.86′ North, 22^{o} 32.37′ West, elevation 1000 feet. The western side of the Paselv valley at the head of Carlsberg Fjord, bounded to the north by Lepidopteriselv, offers an extensive, moderately sloping exposure of the Ørsted Dal Member of the Fleming Fjord Formation with more limited exposure of the Tait Bjerg Beds representing the uppermost part of the formation. Four members of the expedition were dropped off at this site (during the inbound flights to the Macknight Bjerg area, Camp V) for the purpose of re-examining the *Plateosaurus* (Field #4/88G) locality initially discovered in 1988 from which a complete skeleton was excavated in 1989. In addition to collecting fragmentary material from this and one other previously worked site (*Proganochelys*, 22/88G), additional specimens were discovered in both the Tait Bjerg Beds and Ørsted Dal Member. Camp II Quarry, worked for the first time this year, is a fossiliferous horizon in the Ørsted Dal Member which primarily contains disarticulated skeletal elements of the plagiosaurid amphibian *Gerrothorax*; this site also yields other amphibian remains (taxonomic identity as yet undetermined) and fragmentary fish. Of principal interest was the discovery of fragments of a theropod dinosaur (84/91G) in close proximity to the *Plateosaurus* specimen and at the same horizon; with the



exception of their trackways, therapods are rare elements in the Fleming Fjord fauna.

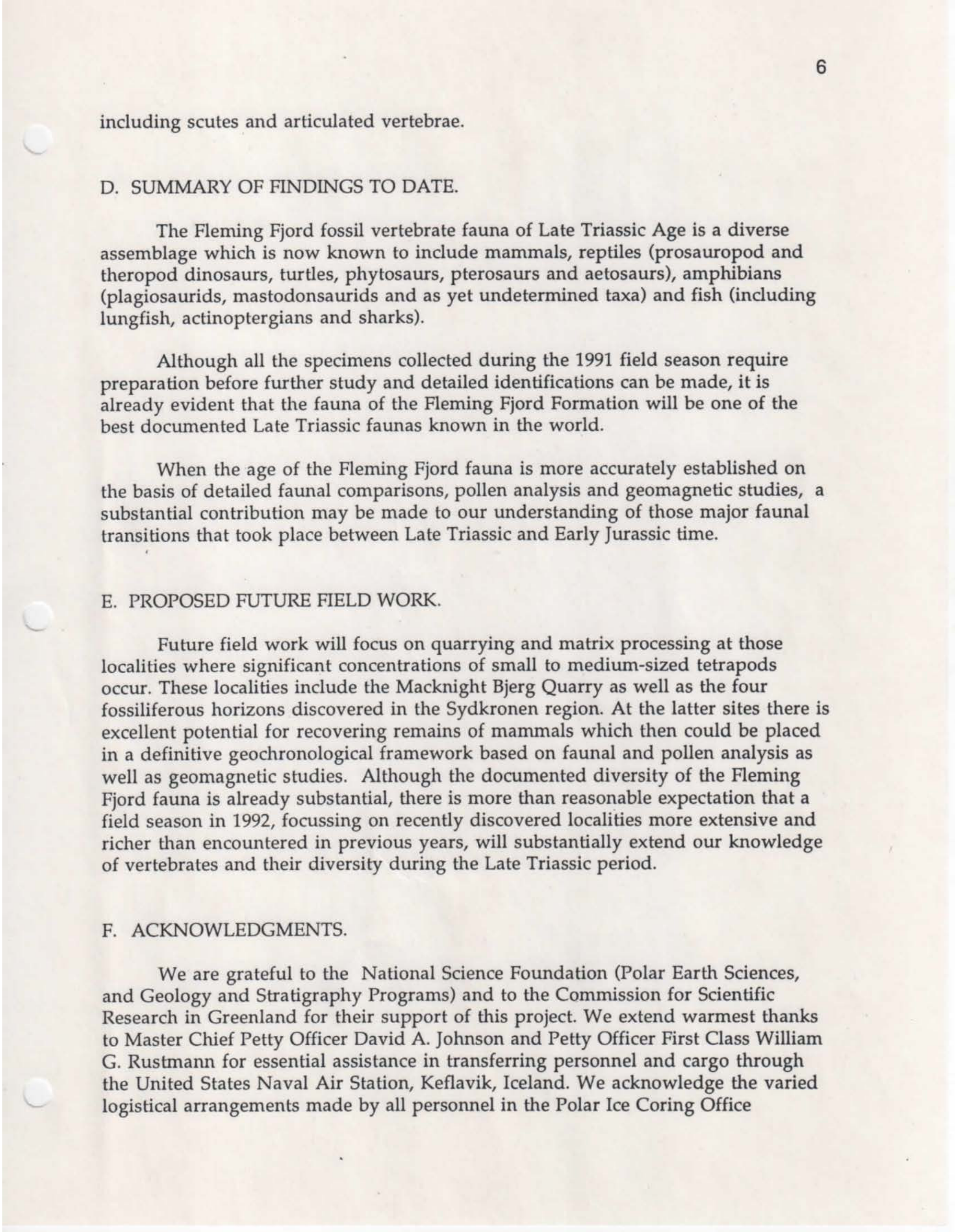
Camp V (10 July - 29 July): 71° 23.24′ North, 22° 34.34′ West, elevation 1,030 feet. This area is bounded to the east by Carlsberg Fjord, to the north by Passagen, to the west by Wood Bjerg and Gule Horn, and to the south by Liaselv. The central topographic feature in this region is Macknight Bjerg, and here and on adjacent mountains are extensive exposures of the Fleming Fjord Formation, and in particular the Malmros Klint and Ørsted Dal Members as well as the Tait Bjerg Beds. Major effort was expended throughout this period on the Macknight Bjerg Quarry (Figure 1, page 16)(located 71·° 22" 30' North, 22° 33" 14' West, elevation 1,110 feet) which yielded an extensive collection of the amphibian *Gerrothorax* (some thirty skulls, and a number of postcranial assemblages). Although *Gerrothorax* and other amphibians are the most common faunal elements at this locality (Figure 2, page 17), disarticulated remains of other tetrapods and fish are also present. These include theropod and prosauropod teeth, reptilian postcranial elements, lungfish teeth, hybodont spines and various jaws of fish and small amphibians; several layers at this site are richly fossiliferous (Figure 3, page 18) The most unexpected find in the Macknight Bjerg Quarry was that of a small, starling-sized ramphorynchoid pterosaur; this diminutive flying reptile is represented by a more or less complete skull with tricuspid teeth as well as a substantial part of the postcranial skeleton. At another locality, some three hundred meters south of Camp V, expeditionary members recovered a well preserved prosauropod skull (Figure 4, page 19) from one of the upper sandstone horizons in the Malmros Klint Member; with the exception of an articulated foot, which was collected, other postcranial elements that are preserved at this site could not be collected at the time due to constraints on the retrograde shipment in terms of both volume and weight. Study of an extensive series of dinosaur tracks at the "Raceway" locality (71° 24.88′ North, 22° 33.17′ West, elevation 1,760 feet) were initiated by Dr. Stephen M. Gatesy (Figure 5, page 20). A partial prosauropod skeleton at this locality, discovered but not collected in 1989 (see Preliminary Report of September 28, 1989, figure 8) was examined by test excavation. This specimen appears to be fragmentary; although a series of poorly preserved caudal vertebrae is present, the scattered, disarticulated preservation of other elements does not offer good prospects for further scientific work.

Camp VI (29 July - 12 August): 71° 28.34′ North, 22° 40.43′ West, elevation 940 feet. An area encompassing the entirety of Tait Bjerg, bounded by Passagen to the south, Buch Bjerg to the north, and Carlsberg Fjord to the east, provides excellent exposures of the Malmros Klint and Ørsted Dal Members as well as the type locality for the Tait Bjerg beds at the summit of the mountain (Figure 6, page 21). A number of bone bearing horizons as well as specimens *in situ* discovered in 1989 were reexamined in detail for collection. The major discovery made in this area was a mammalian premolariform tooth, representing the first evidence of Mesozoic mammals from Greenland (Figure 7, page 22). Isolated teeth of Late Triassic mammals are known from a few localities in the world, but are extremely rare. The documented presence of mammals in Late Triassic sediments in Greenland substantially raises expectations that more complete material may be recovered from East Greenland in the future. The specimen was preserved in a thin bonebed with a lateral extent of only 20 meters; identifiable remains of other vertebrates include prosauropod and theropod dinosaurs, ?phytosaur teeth, amphibians (*Gerrothorax*, *Mastodonsaurus*), and various fish (including lungfish and hybodont sharks). Dr. Gatesy continued his studies of dinosaur trackways which occur both in the Ørsted Dal and Tait Bjerg Beds, and Dr. Lars B. Clemmensen undertook various stratigraphic sections to document the position of vertebrate localities as well as horizons bearing dinosaur trackways. Drs. Shubin and Clemmensen also collected a series of rock samples for pollen analysis which may provide additional evidence on the age of the Fleming Fjord Formation. The amphibian *Gerrothorax*, which occurs in both the Ørsted Dal and Malmros Klint members, was found to extend to the uppermost part of the section in the Tait Bjerg Beds exposed two kilometers west of Tait Bjerg itself. A prosauropod dinosaur discovered in 1989 in one of the uppermost sandstone horizons of the Malmros Klint Member was excavated and examined for diagnostic cranial features but none were found; parts of this skeleton were collected by Mr. Niels Bonde for instructional purposes at the University of Copenhagen. On the last day of operations in the Camp VI area another dinosaur skeleton, probably a prosauropod, was discovered in the Malmros Klint Member approximately 200 meters north of Camp VI; this specimen awaits excavation and detailed examination in the future.

For the final phase of the field season the expedition was divided to undertake reconnaissance in different areas, with a view towards locating fossiliferous deposits representing more terrestrial regimes closer to the western source area of the Triassic rift valley.

Camp VII (12 August - 18 August): 71° 44.10′ North, 23° 11.37′ West, elevation 600 feet (estimated). An extensive area comprising Schröter Bjerge, bounded by Ørsted Dal on the north, Allday Dal to the west, Solfadsdal to the east, and Malmros Klint and Fleming Fjord to the south. Exposures of the Fleming Fjord and Kap Stewart Formations in this area are discontinuous, highly faulted, often deeply weathered or covered by skree. Expeditionary members undertook a complete reconnaissance of this region, and determined that the exposures offered poor prospect for further paleontological investigation.

Camp VIII (12 August - 18 August): 71° 49.65′ North, 23° 30.83′ West, elevation 1,760 feet. The rugged terrain of Sydkronen, bounded by Ørsted Dal to the south and Gipsdalen to the west, was discovered to offer outstanding exposures of the Fleming Fjord Formation as well as the possibility of reconnaissance of Middle-Triassic sediments to the west. No less than four extensive and richly fossiliferous horizons were discovered which, in addition to taxa known from other localities (e.g., *Gerrothorax* and other amphibians) preserved faunal elements that had previously not been found and which are possibly indicative of a more terrestrial regime. Among these are large, gar-like scales and a partial aetosaur skeleton,



including scutes and articulated vertebrae.

D. SUMMARY OF FINDINGS TO DATE.

The Fleming Fjord fossil vertebrate fauna of Late Triassic Age is a diverse assemblage which is now known to include mammals, reptiles (prosauropod and theropod dinosaurs, turtles, phytosaurs, pterosaurs and aetosaurs), amphibians (plagiosaurids, mastodonsaurids and as yet undetermined taxa) and fish (including lungfish, actinoptergians and sharks).

Although all the specimens collected during the 1991 field season require preparation before further study and detailed identifications can be made, it is already evident that the fauna of the Fleming Fjord Formation will be one of the best documented Late Triassic faunas known in the world.

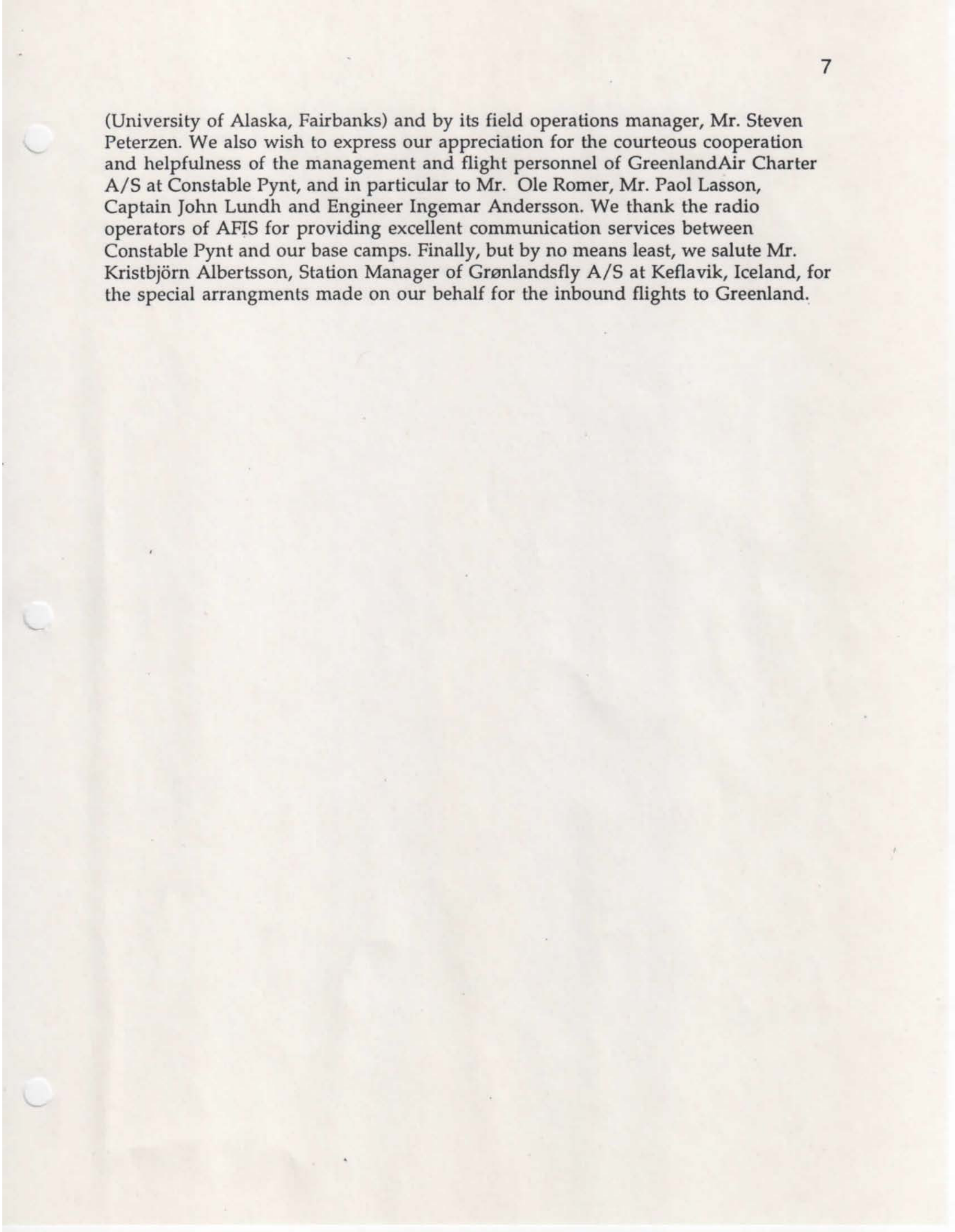
When the age of the Fleming Fjord fauna is more accurately established on the basis of detailed faunal comparisons, pollen analysis and geomagnetic studies, a substantial contribution may be made to our understanding of those major faunal transitions that took place between Late Triassic and Early Jurassic time.

E. PROPOSED FUTURE FIELD WORK.

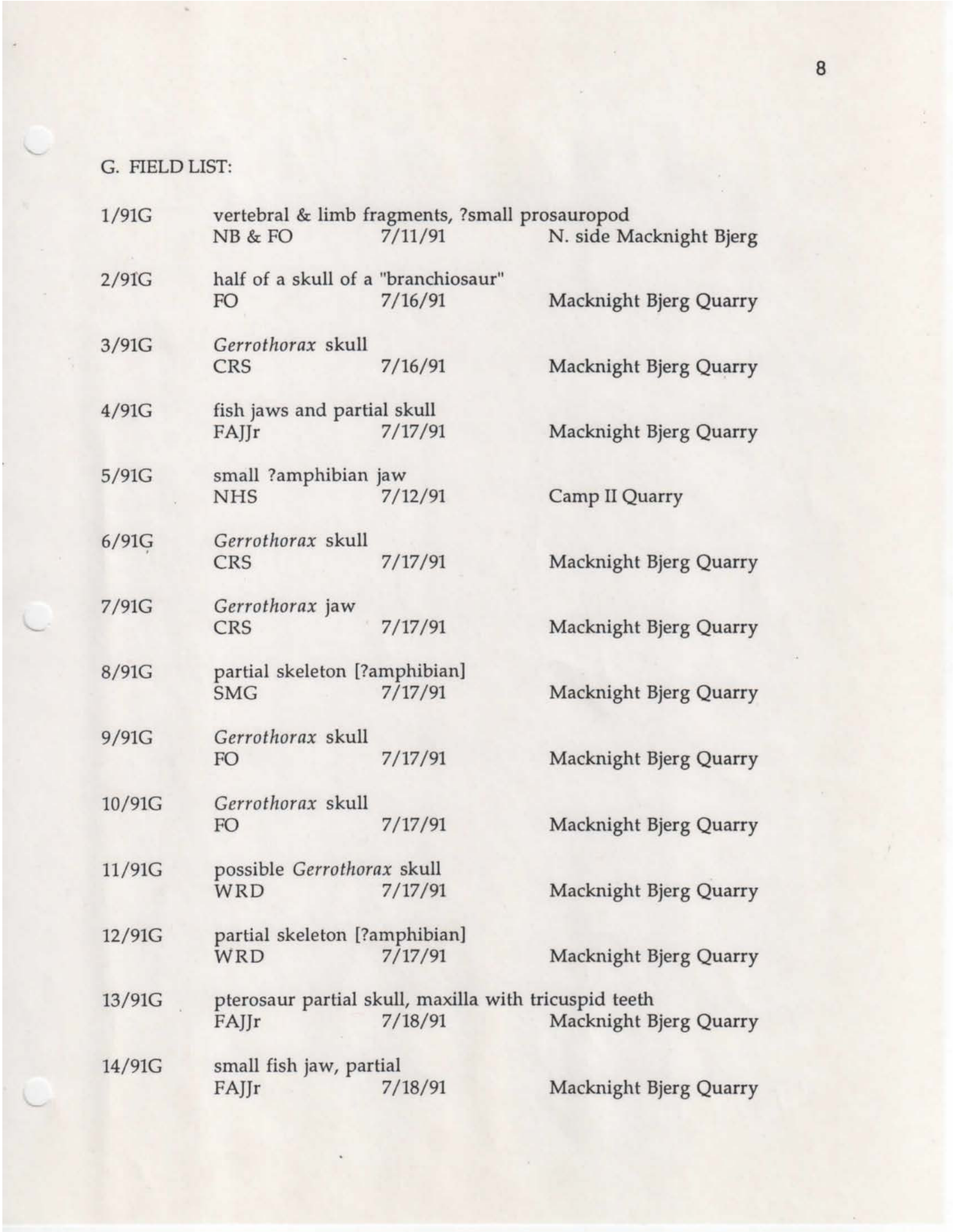
Future field work will focus on quarrying and matrix processing at those localities where significant concentrations of small to medium-sized tetrapods occur. These localities include the Macknight Bjerg Quarry as well as the four fossiliferous horizons discovered in the Sydkronen region. At the latter sites there is excellent potential for recovering remains of mammals which then could be placed in a definitive geochronological framework based on faunal and pollen analysis as well as geomagnetic studies. Although the documented diversity of the Fleming Fjord fauna is already substantial, there is more than reasonable expectation that a field season in 1992, focussing on recently discovered localities more extensive and richer than encountered in previous years, will substantially extend our knowledge of vertebrates and their diversity during the Late Triassic period.

F. ACKNOWLEDGMENTS.

We are grateful to the National Science Foundation (Polar Earth Sciences, and Geology and Stratigraphy Programs) and to the Commission for Scientific Research in Greenland for their support of this project. We extend warmest thanks to Master Chief Petty Officer David A. Johnson and Petty Officer First Class William G. Rustmann for essential assistance in transferring personnel and cargo through the United States Naval Air Station, Keflavik, Iceland. We acknowledge the varied logistical arrangements made by all personnel in the Polar Ice Coring Office

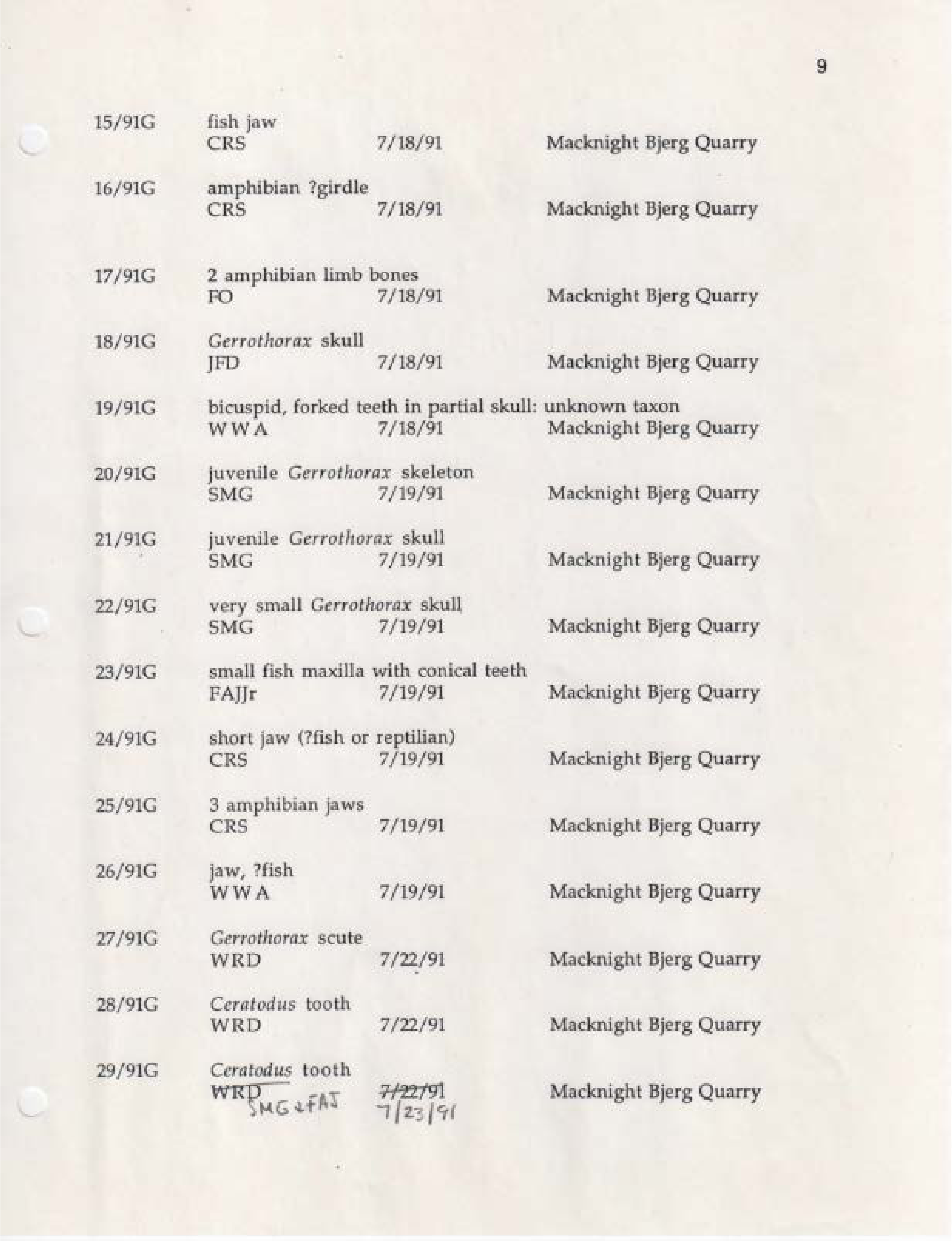


(University of Alaska, Fairbanks) and by its field operations manager, Mr. Steven Peterzen. We also wish to express our appreciation for the courteous cooperation and helpfulness of the management and flight personnel of GreenlandAir Charter A/S at Constable Pynt, and in particular to Mr. Ole Romer, Mr. Paol Lasson, Captain John Lundh and Engineer Ingemar Andersson. We thank the radio operators of AFIS for providing excellent communication services between Constable Pynt and our base camps. Finally, but by no means least, we salute Mr. Kristbjörn Albertsson, Station Manager of Grønlandsfly A/S at Keflavik, Iceland, for the special arrangments made on our behalf for the inbound flights to Greenland.

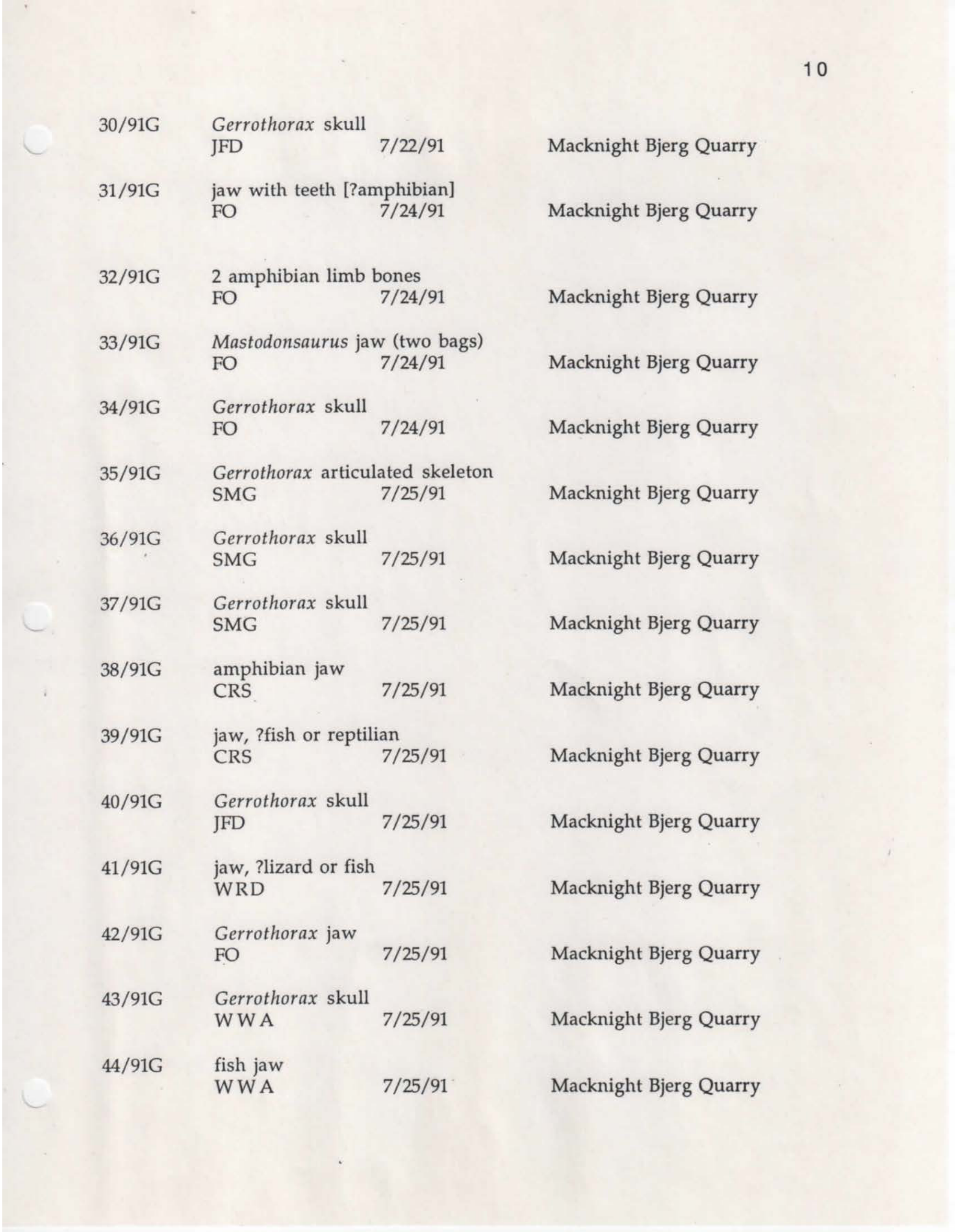


G. FIELD LIST:

1/91G	vertebral & limb fragments, ?small prosauropod	NB & FO	7/11/91	N. side Macknight Bjerg
2/91G	half of a skull of a "branchiosaur"	FO	7/16/91	Macknight Bjerg Quarry
3/91G	*Gerrothorax* skull	CRS	7/16/91	Macknight Bjerg Quarry
4/91G	fish jaws and partial skull	FAJJr	7/17/91	Macknight Bjerg Quarry
5/91G	small ?amphibian jaw	NHS	7/12/91	Camp II Quarry
6/91G	*Gerrothorax* skull	CRS	7/17/91	Macknight Bjerg Quarry
7/91G	*Gerrothorax* jaw	CRS	7/17/91	Macknight Bjerg Quarry
8/91G	partial skeleton [?amphibian]	SMG	7/17/91	Macknight Bjerg Quarry
9/91G	*Gerrothorax* skull	FO	7/17/91	Macknight Bjerg Quarry
10/91G	*Gerrothorax* skull	FO	7/17/91	Macknight Bjerg Quarry
11/91G	possible *Gerrothorax* skull	WRD	7/17/91	Macknight Bjerg Quarry
12/91G	partial skeleton [?amphibian]	WRD	7/17/91	Macknight Bjerg Quarry
13/91G	pterosaur partial skull, maxilla with tricuspid teeth	FAJJr	7/18/91	Macknight Bjerg Quarry
14/91G	small fish jaw, partial	FAJJr	7/18/91	Macknight Bjerg Quarry



15/91G	fish jaw CRS	7/18/91	Macknight Bjerg Quarry
16/91G	amphibian ?girdle CRS	7/18/91	Macknight Bjerg Quarry
17/91G	2 amphibian limb bones FO	7/18/91	Macknight Bjerg Quarry
18/91G	*Gerrothorax* skull JFD	7/18/91	Macknight Bjerg Quarry
19/91G	bicuspid, forked teeth in partial skull: unknown taxon WWA	7/18/91	Macknight Bjerg Quarry
20/91G	juvenile *Gerrothorax* skeleton SMG	7/19/91	Macknight Bjerg Quarry
21/91G	juvenile *Gerrothorax* skull SMG	7/19/91	Macknight Bjerg Quarry
22/91G	very small *Gerrothorax* skull SMG	7/19/91	Macknight Bjerg Quarry
23/91G	small fish maxilla with conical teeth FAJJr	7/19/91	Macknight Bjerg Quarry
24/91G	short jaw (?fish or reptilian) CRS	7/19/91	Macknight Bjerg Quarry
25/91G	3 amphibian jaws CRS	7/19/91	Macknight Bjerg Quarry
26/91G	jaw, ?fish WWA	7/19/91	Macknight Bjerg Quarry
27/91G	*Gerrothorax* scute WRD	7/22/91	Macknight Bjerg Quarry
28/91G	*Ceratodus* tooth WRD	7/22/91	Macknight Bjerg Quarry
29/91G	*Ceratodus* tooth ~~WRD~~ SMG & FAJ	~~7/22/91~~ 7/23/91	Macknight Bjerg Quarry



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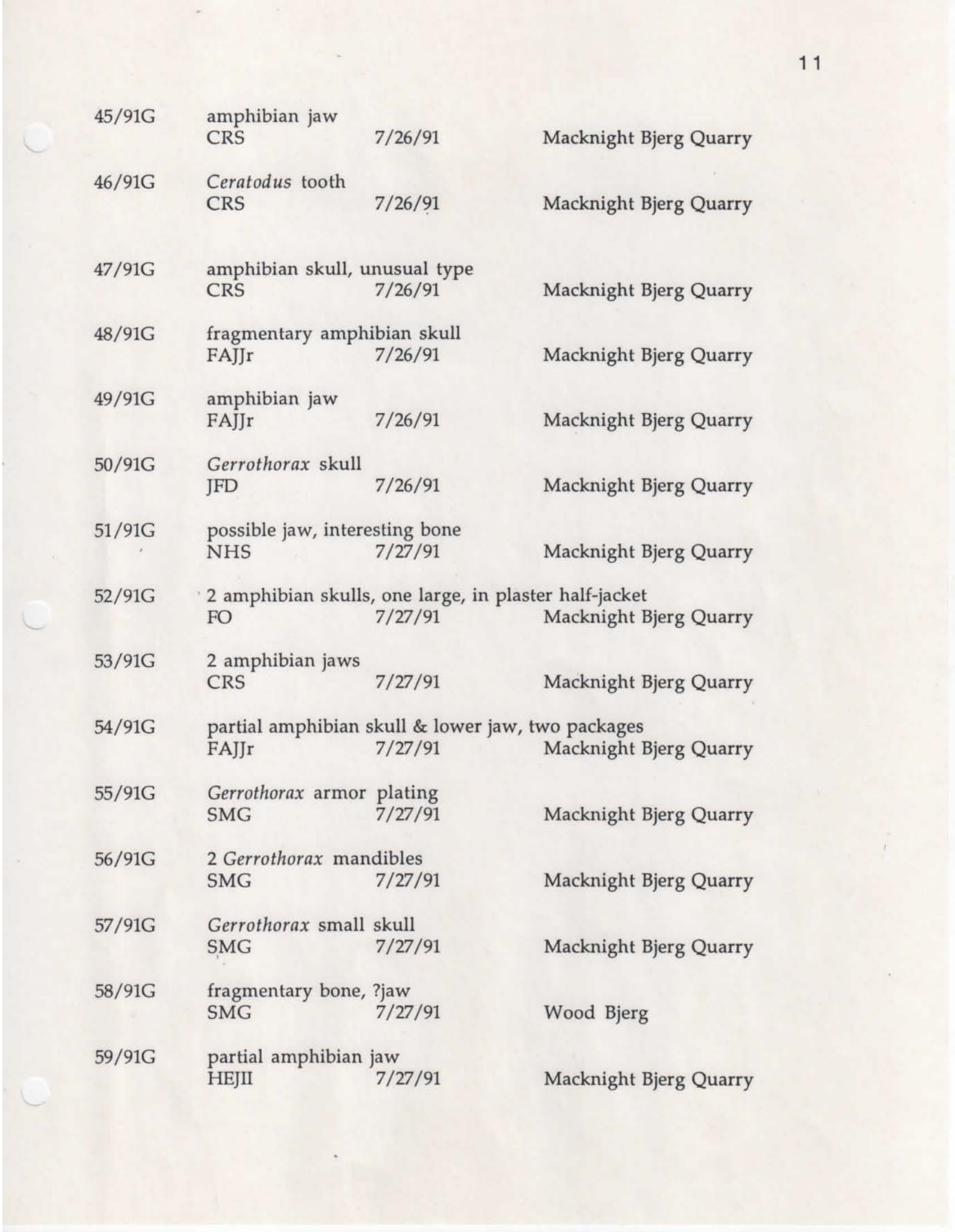
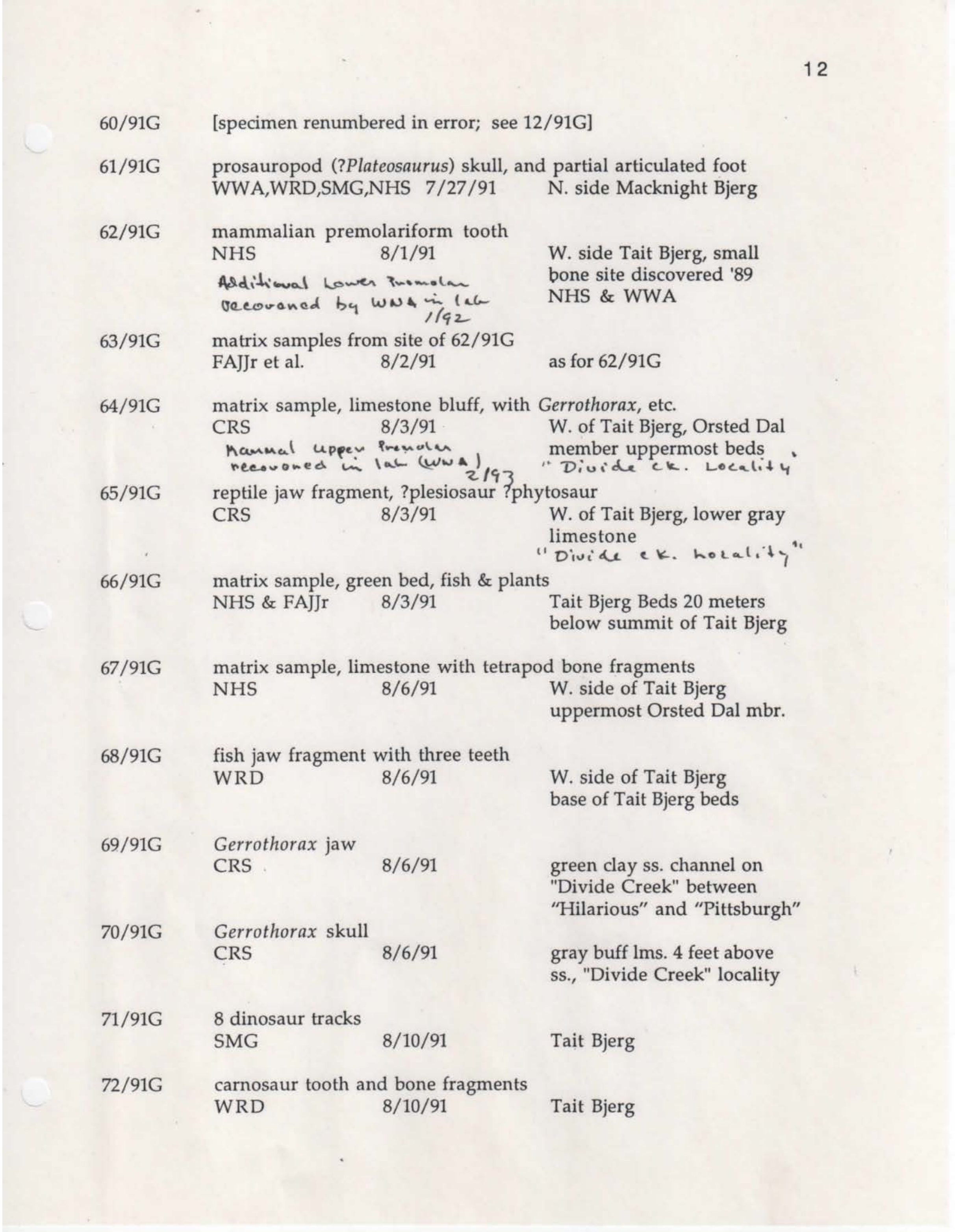
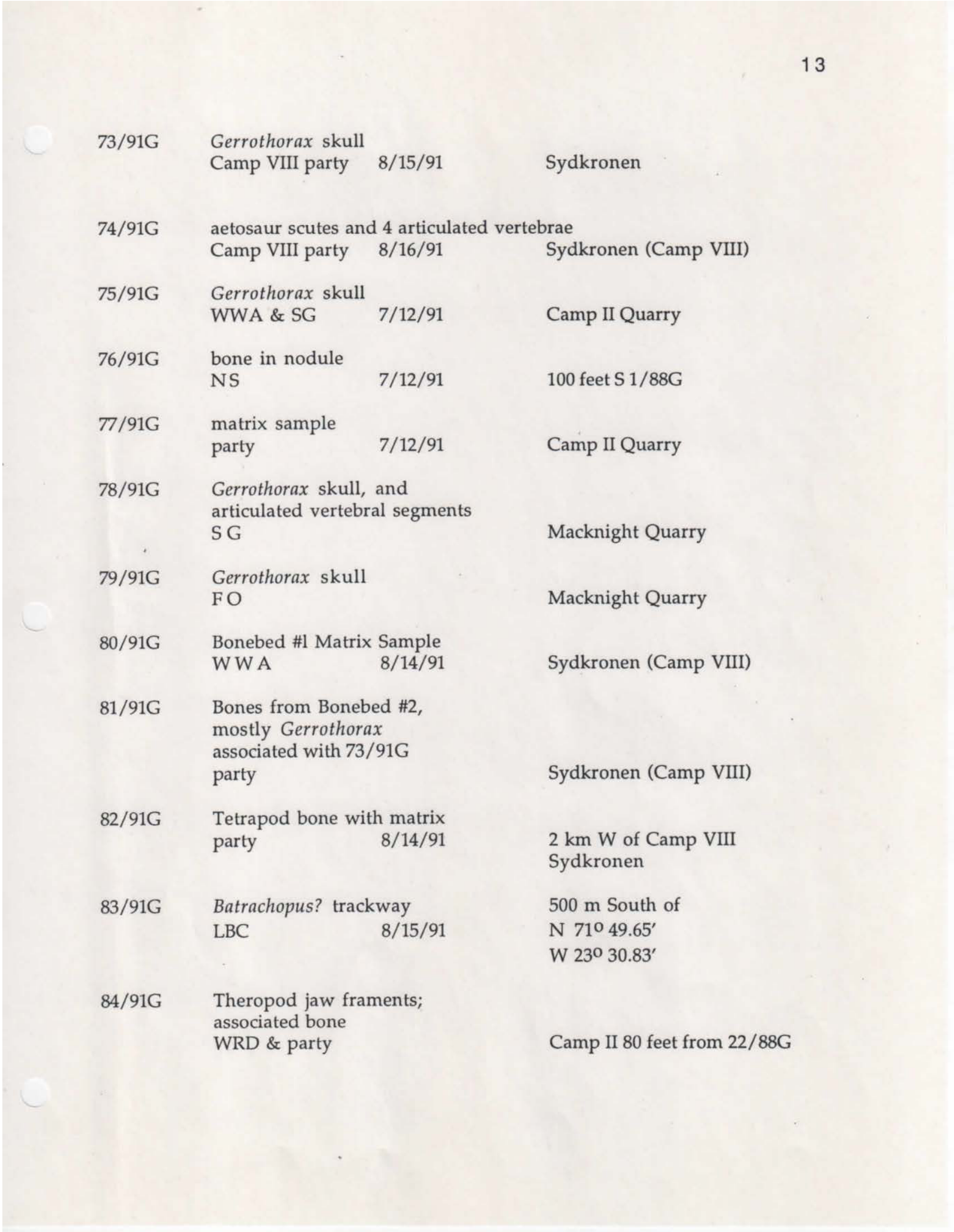
30/91G	*Gerrothorax* skull JFD	7/22/91	Macknight Bjerg Quarry
31/91G	jaw with teeth [?amphibian] FO	7/24/91	Macknight Bjerg Quarry
32/91G	2 amphibian limb bones FO	7/24/91	Macknight Bjerg Quarry
33/91G	*Mastodonsaurus* jaw (two bags) FO	7/24/91	Macknight Bjerg Quarry
34/91G	*Gerrothorax* skull FO	7/24/91	Macknight Bjerg Quarry
35/91G	*Gerrothorax* articulated skeleton SMG	7/25/91	Macknight Bjerg Quarry
36/91G	*Gerrothorax* skull SMG	7/25/91	Macknight Bjerg Quarry
37/91G	*Gerrothorax* skull SMG	7/25/91	Macknight Bjerg Quarry
38/91G	amphibian jaw CRS	7/25/91	Macknight Bjerg Quarry
39/91G	jaw, ?fish or reptilian CRS	7/25/91	Macknight Bjerg Quarry
40/91G	*Gerrothorax* skull JFD	7/25/91	Macknight Bjerg Quarry
41/91G	jaw, ?lizard or fish WRD	7/25/91	Macknight Bjerg Quarry
42/91G	*Gerrothorax* jaw FO	7/25/91	Macknight Bjerg Quarry
43/91G	*Gerrothorax* skull WWA	7/25/91	Macknight Bjerg Quarry
44/91G	fish jaw WWA	7/25/91	Macknight Bjerg Quarry



45/91G	amphibian jaw CRS	7/26/91	Macknight Bjerg Quarry
46/91G	*Ceratodus* tooth CRS	7/26/91	Macknight Bjerg Quarry
47/91G	amphibian skull, unusual type CRS	7/26/91	Macknight Bjerg Quarry
48/91G	fragmentary amphibian skull FAJJr	7/26/91	Macknight Bjerg Quarry
49/91G	amphibian jaw FAJJr	7/26/91	Macknight Bjerg Quarry
50/91G	*Gerrothorax* skull JFD	7/26/91	Macknight Bjerg Quarry
51/91G	possible jaw, interesting bone NHS	7/27/91	Macknight Bjerg Quarry
52/91G	2 amphibian skulls, one large, in plaster half-jacket FO	7/27/91	Macknight Bjerg Quarry
53/91G	2 amphibian jaws CRS	7/27/91	Macknight Bjerg Quarry
54/91G	partial amphibian skull & lower jaw, two packages FAJJr	7/27/91	Macknight Bjerg Quarry
55/91G	*Gerrothorax* armor plating SMG	7/27/91	Macknight Bjerg Quarry
56/91G	2 *Gerrothorax* mandibles SMG	7/27/91	Macknight Bjerg Quarry
57/91G	*Gerrothorax* small skull SMG	7/27/91	Macknight Bjerg Quarry
58/91G	fragmentary bone, ?jaw SMG	7/27/91	Wood Bjerg
59/91G	partial amphibian jaw HEJII	7/27/91	Macknight Bjerg Quarry



60/91G	[specimen renumbered in error; see 12/91G]			
61/91G	prosauropod (?*Plateosaurus*) skull, and partial articulated foot	WWA,WRD,SMG,NHS	7/27/91	N. side Macknight Bjerg
62/91G	mammalian premolariform tooth Additional Lower Premolar recovered by WWA in lab 1/92	NHS	8/1/91	W. side Tait Bjerg, small bone site discovered '89 NHS & WWA
63/91G	matrix samples from site of 62/91G	FAJJr et al.	8/2/91	as for 62/91G
64/91G	matrix sample, limestone bluff, with *Gerrothorax*, etc. Mammal upper Premolar recovered in lab (WWA) 2/93	CRS	8/3/91	W. of Tait Bjerg, Orsted Dal member uppermost beds "Divide ck. Locality"
65/91G	reptile jaw fragment, ?plesiosaur ?phytosaur	CRS	8/3/91	W. of Tait Bjerg, lower gray limestone "Divide ck. Locality"
66/91G	matrix sample, green bed, fish & plants	NHS & FAJJr	8/3/91	Tait Bjerg Beds 20 meters below summit of Tait Bjerg
67/91G	matrix sample, limestone with tetrapod bone fragments	NHS	8/6/91	W. side of Tait Bjerg uppermost Orsted Dal mbr.
68/91G	fish jaw fragment with three teeth	WRD	8/6/91	W. side of Tait Bjerg base of Tait Bjerg beds
69/91G	*Gerrothorax* jaw	CRS	8/6/91	green clay ss. channel on "Divide Creek" between "Hilarious" and "Pittsburgh"
70/91G	*Gerrothorax* skull	CRS	8/6/91	gray buff lms. 4 feet above ss., "Divide Creek" locality
71/91G	8 dinosaur tracks	SMG	8/10/91	Tait Bjerg
72/91G	carnosaur tooth and bone fragments	WRD	8/10/91	Tait Bjerg



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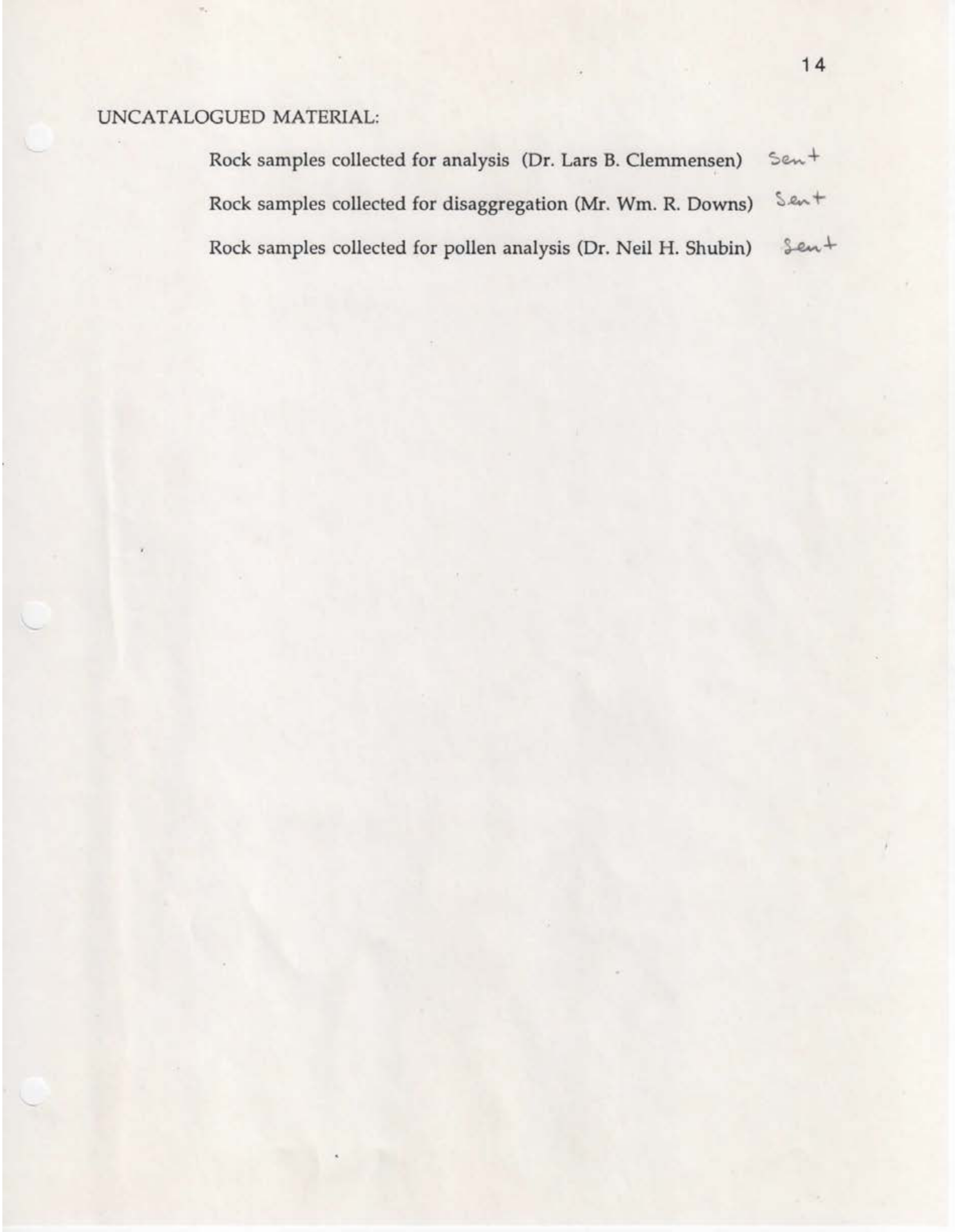
73/91G	*Gerrothorax* skull Camp VIII party	8/15/91	Sydkronen
74/91G	aetosaur scutes and 4 articulated vertebrae Camp VIII party	8/16/91	Sydkronen (Camp VIII)
75/91G	*Gerrothorax* skull WWA & SG	7/12/91	Camp II Quarry
76/91G	bone in nodule NS	7/12/91	100 feet S 1/88G
77/91G	matrix sample party	7/12/91	Camp II Quarry
78/91G	*Gerrothorax* skull, and articulated vertebral segments SG		Macknight Quarry
79/91G	*Gerrothorax* skull FO		Macknight Quarry
80/91G	Bonebed #l Matrix Sample WWA	8/14/91	Sydkronen (Camp VIII)
81/91G	Bones from Bonebed #2, mostly *Gerrothorax* associated with 73/91G party		Sydkronen (Camp VIII)
82/91G	Tetrapod bone with matrix party	8/14/91	2 km W of Camp VIII Sydkronen
83/91G	*Batrachopus?* trackway LBC	8/15/91	500 m South of N 71° 49.65′ W 23° 30.83′
84/91G	Theropod jaw framents; associated bone WRD & party		Camp II 80 feet from 22/88G



UNCATALOGUED MATERIAL:

Rock samples collected for analysis (Dr. Lars B. Clemmensen)	Sent
Rock samples collected for disaggregation (Mr. Wm. R. Downs)	Sent
Rock samples collected for pollen analysis (Dr. Neil H. Shubin)	Sent

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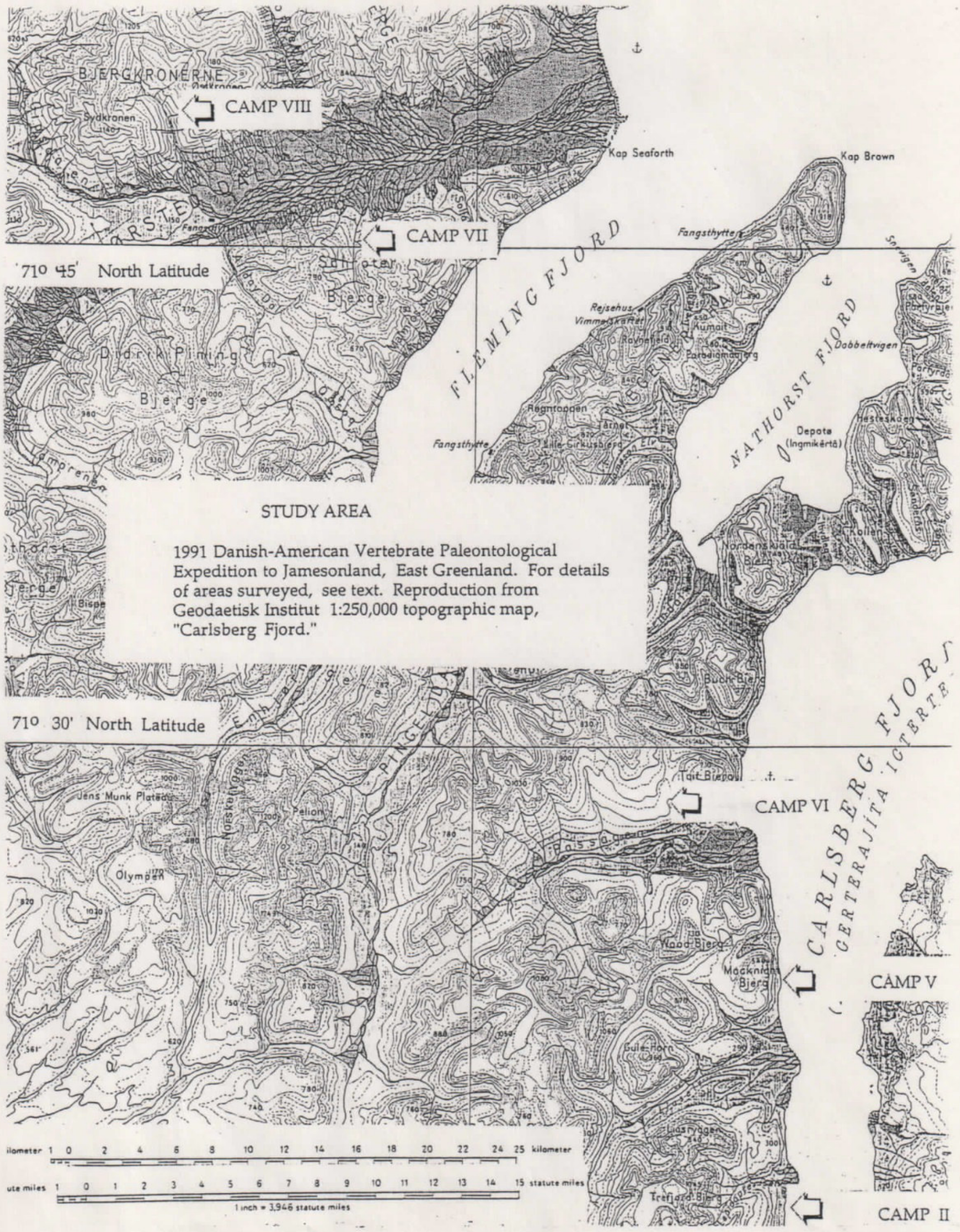


STUDY AREA

1991 Danish-American Vertebrate Paleontological Expedition to Jamesonland, East Greenland. For details of areas surveyed, see text. Reproduction from Geodaetisk Institut 1:250,000 topographic map, "Carlsberg Fjord."

Figure 1. The Macknight Bjerg Quarry. A major part of the Expedition's effort was directed at quarrying the several richly fossiliferous horizons at this locality.

Figure 2. Mr. Frank Osbæck excavating two amphibian skulls, preserved overlapping one another, in the Macknight Bjerg Quarry.

Figure 3. A sample of the richly fossiliferous matrix from the Macknight Bjerg Quarry showing a large coprolite (center), a limb bone (upper left), a theropod tooth (lower center) and other bones.

Figure 4. The skull of a prosauropod dinosaur (probably *Plateosaurus*) shown in this photograph shortly after its discovery. The specimen, which includes elements of the postcranial skeleton, was found in a sandstone channel of the upper Malmrose Kint member; the rock at this locality lacks well defined bedding planes that cleave easily, making collection difficult.

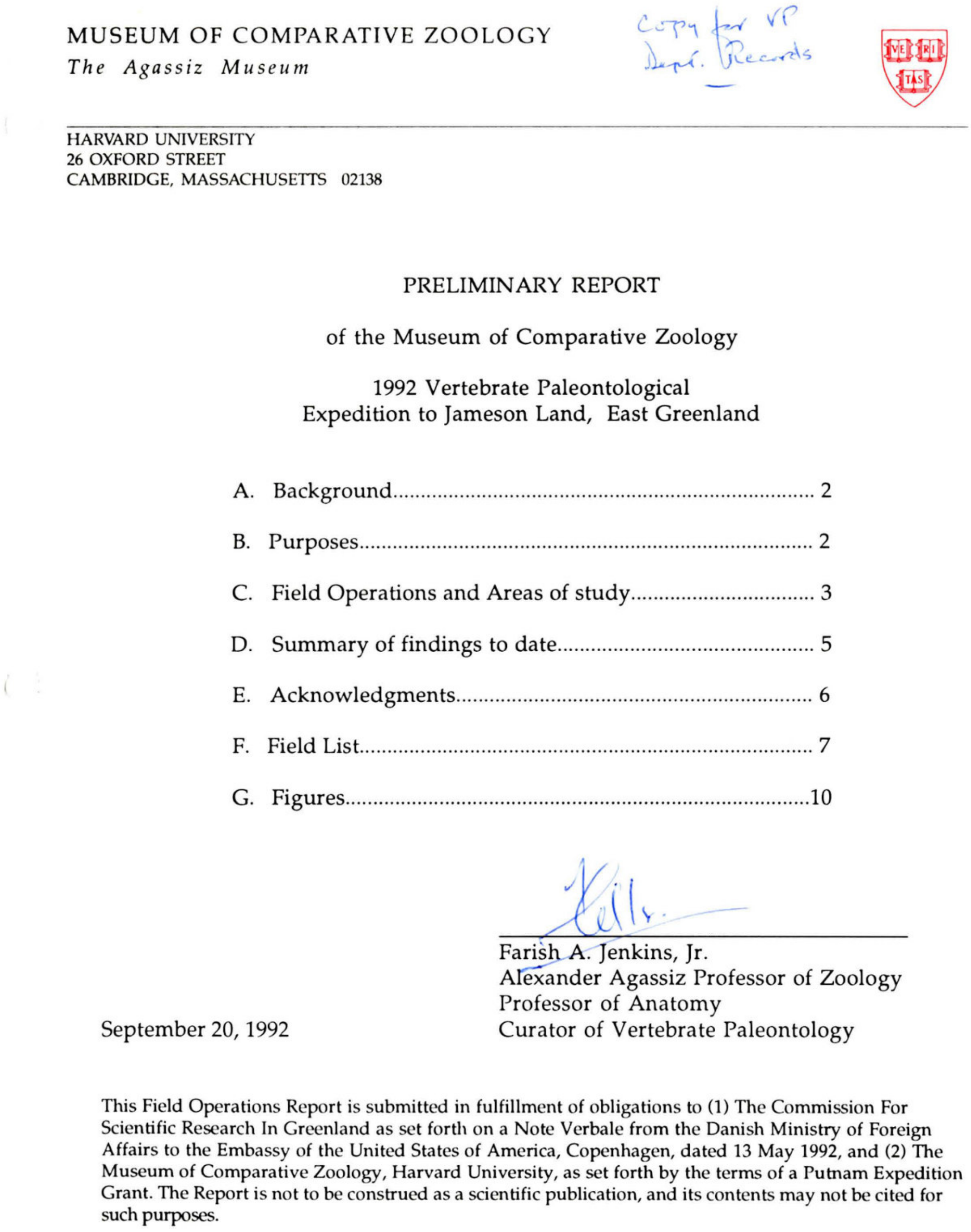
Figure 5. The three-toed trackway of a theropod dinosaur at the "Raceway" locality north of Macknight Bjerg. The stride length of the dinosaur is indicated by length of the handle of the Marsh pick (ca. 1 meter).

Figure 6. Panoramic view of outcrops of the Fleming Fjord Formation (Camp VI area). On the left is the western slope of Tait Bjerg where a mammalian premolariform tooth was discovered. Across the valley of Passagen and along the horizon on the right is the "Raceway" dinosaur track locality. Carlsberg Fjord and Liverpool Land are seen in the background.

Figure 7. Stereophotograph of a mammalian premolariform tooth, the first evidence of Late Triassic mammals from Greenland. The tooth, which has a crown length of about 1.5 mm, is probably equivalent in age to the earliest known mammals in the world.

A8 – Field report 1992 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1992 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



MUSEUM OF COMPARATIVE ZOOLOGY
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PRELIMINARY REPORT

of the Museum of Comparative Zoology

1992 Vertebrate Paleontological
Expedition to Jameson Land, East Greenland

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Farish A. Jenkins, Jr.
Alexander Agassiz Professor of Zoology
Professor of Anatomy
Curator of Vertebrate Paleontology

September 20, 1992

This Field Operations Report is submitted in fulfillment of obligations to (1) The Commission For Scientific Research In Greenland as set forth on a Note Verbale from the Danish Ministry of Foreign Affairs to the Embassy of the United States of America, Copenhagen, dated 13 May 1992, and (2) The Museum of Comparative Zoology, Harvard University, as set forth by the terms of a Putnam Expedition Grant. The Report is not to be construed as a scientific publication, and its contents may not be cited for such purposes.

A. BACKGROUND

The 1992 Vertebrate Paleontological Expedition to East Greenland was conducted with the financial assistance of a research grant from the U.S. National Science Foundation (Grant #EAR-9204789), a Putnam Expedition Grant from the Museum of Comparative Zoology, and with the permission of the Danish Commission for Scientific Research in Greenland. Additional assistance was provided to Dr. Lars B. Clemmensen by The Carlsberg Foundation (Copenhagen). This expedition, the fourth field season spent in Jamesonland (see Reports previously submitted for 1988, 1989 and 1991), operated for a period of forty days from 25 June through 4 August, 1992. The expedition was led by Professor Farish A. Jenkins, Jr., and staffed by: Mr. William W. Amaral, Mr. Charles R. Schaff, and Ms. Amy R. Davidson (Harvard University); Dr. Neil H. Shubin (University of Pennsylvania); Dr. Stephen M. Gatesy (University of Montana); Dr. Lars B. Clemmensen (University of Copenhagen); Mr. William R. Downs (Northern Arizona University); and Dr. Dennis V. Kent (Lamont-Doherty Geological Observatory, Columbia University).

This investigation was made possible by the extensive sedimentological and stratigraphic analyses undertaken by previous researchers, most notably K. Perch-Nielsen et al. (1972, 1974) and Lars B. Clemmensen (1980a, b). More recent work by Dr. Gregers Dam has focused on a lithofacies analysis of the Triassic and Jurassic rocks in this region, and includes palynology, ichnology, source rock and porosity/permeability analyses (Dam, 1988). Prior to the first MCZ-Harvard paleontological expedition in 1988, no fossil tetrapods of substantial scientific significance had ever been recovered from Late Triassic sediments in Greenland.

B. PURPOSES

A primary goal of the project was to collect fossils essential to understanding vertebrate faunal evolution during the Late Triassic, which includes the origin of mammals as well as other major tetrapod groups (e.g., dinosaurs, turtles, crocodylomorphs, pterosaurs). Although major originations took place during this time, almost half of known Late Triassic tetrapod families became extinct by the Early Jurassic. The temporal, taxonomic and geographic extent of this faunal turnover has been debated, principally because well-dated, fossiliferous rock sequences are rare. The Late Triassic Fleming Fjord Formation offers a greater range of rock types (representing lacustrine, fluviatile and subaerial environments) than those in which Late Triassic faunas have previously been found.

A second goal of the 1992 expedition was to extend exploration into different facies and stratigraphic levels. East Greenland offers the very rare occurence of a complete section of well exposed, continental sediments spanning from the Middle Triassic to Early Jurassic. Clemmensen (1980a) described some thirteen main facies associations represented in the East Greenland Triassic rift basin. Our field work to date has focused principally on the red mudstone association of the Malmros Klint member, the red mudstone-grey sandstone of the Ørsted Dal member, and the light-colored carbonate rock association of the Tait Bjerg beds, all typically developed in the central part of the basin. Several of these associations, however, vary laterally toward the western source area and presented the opportunity to examine more depositional environments than are represented in the central basin. Thus, with its exceptional exposure, the Fleming Fjord Formation offered the opportunity to examine a range of facies over a greater geographic and temporal extent than at European localities, which are relatively restricted.

A third goal was to facilitate geological studies that would place the Greenlandic fauna in a global statigraphic framework. For this purpose we invited Dr. Dennis V. Kent to join the expedition to conduct sampling for paleomagnetic analysis that might provide correlation with the Newark Supergroup of eastern North America. The Fleming Fjord Formation is nominally coeval with and of similar lithologic character as the Passaic Formation of the Newark Supergroup (Middle Triassic to Early Jurassic). Newark rift sediments have proven to be excellent paleomagnetic recorders and have permitted the development of a stratigraphic framework based on geomagnetic polarity from available outcrop samples (Witte et al., 1991). More recently, practically the entire Newark section has been recovered in a cumulative total of 20,000 feet of continuous cores from six drilling sites (NSF-sponsored Newark Basin Coring Project; Olsen and Kent, 1990). Thus far, data from over 900 samples (from three cores) that have been analyzed in detail provide evidence of a coherent pattern of normal and reversed polarity magnetozones; these magnetozones can be correlated over much of the basin and are congruent with the polarity framework based on outcrop samples (Dennis V. Kent, personal communication). By developing a magnetostratigraphy for the Fleming Fjord Formation and correlating the magnetozones to the well-defined history of geomagnetic polarities that is chronicled in the Newark sequence, the Fleming Fjord fauna, which includes many taxa known from various European deposits, might thus become known as a significant biostratigraphic link between Europe and North America.

C. FIELD OPERATIONS AND AREAS OF STUDY

Paleontological reconnaissance, excavation and collecting were undertaken from three base camps in which the surrounding areas were surveyed; all of these areas lie within the southern half of the Triassic rift valley basin as interpreted by L.B. Clemmenson. During the first two weeks the expedition was divided between Camps V and VI, areas that previously had been studied but which offered further opportunities for scientific return. During the last three weeks the entire expedition's effort was focused on the largely unexplored area surrounding Camp IX.

An unexpected and serious impediment to executing the original field operations plan was the residual snow from what was represented as the worst winter in Greenlandic memory. In areas worked during the previous three summer seasons where there had been typically only 15% or less snow cover, members of the expedition were confronted with coverage of between 50-90% on the outcrops of interest (Figure 1). Additionally, modifications of the field plan had to be made both at the beginning and end of the field season due to the operational (principally pay load) constraints of the Bell 206 GreenlandAir helicopter.

Camp II : 71° 15.86' North, 22° 32.37' West, elevation 1000 feet. The western side of the Paselv valley at the head of Carlsberg Fjord, bounded to the north by Lepidopteriselv, offers an extensive, moderately sloping exposure of the Ørsted Dal Member of the Fleming Fjord Formation with more limited exposure of the Tait Bjerg Beds representing the uppermost part of the formation. Scheduled operations in the area were cancelled due to the 90% snow cover in early July; melting during the first three weeks of July reduced the coverage only to 75%.

Camp V (30 June - 13 July; FAJJr, CRS, SMG, WRD, ARD): 71° 23.24' North, 22° 34.34' West, elevation 1,030 feet. This area is bounded to the east by Carlsberg Fjord, to the north by Passagen, to the west by Wood Bjerg and Gule Horn, and to the south by Liaselv. The central topographic feature in this region is Macknight Bjerg, and here and on adjacent mountains are extensive exposures of the Fleming Fjord Formation, and in particular the Malmros Klint and Ørsted Dal Members as well as the Tait Bjerg Beds. Snow coverage on Macknight Berg was initially about 50% on the north side and 90% on the south side. Given that these conditions prevented any sustained prospecting effort as originally planned, the Macknight Bjerg Quarry (located 71° 22. 30' North, 22° 33.14' West, elevation 1,110 feet) was relocated by a GPS monitor and dug out. In 1991 a major effort was made at this site which yielded an extensive collection of amphibians and a nearly complete skeleton of the primitive pterosaur *Eudimorphodon*, and the quarry continued to prove fossiliferous this year. In addition to the expected array of small amphibians, fish and disarticulated reptilian remains, the most significant find was that of a large (.5 meter from tip of snout to occiput), well preserved amphibian skull (Figure 2). In addition, a number of specimens of the broad-headed amphibian *Gerrothorax* were collected, some with associated postcranial elements (Figure 3). Dr. Stephen M. Gatesy completed a survey of the extensive exposures of dinosaur tracks on the eastern shoulder of Wood Bjerg. at the "Raceway" locality (71° 24.88' North, 22° 33.17' West, elevation 1,760 feet) which was discovered during the 1989 field season. Mapping of 225m^2 of exposed surface revealed a minimum of 52 different trackways, consisting of up to 24 consecutive footprints (Figure 4). Detailed maps were also made of small sections containing unusual grooves that we interpret as tail-drags. Exceptionally preserved prints with foot pad skin impressions were discovered in this same layer. Much of Dr. Gatesy's effort was aimed at documenting variation in track morphology along a single sedimentary layer. Forty-eight trackways distributed along the 230m long transect were photographed (Figure 5), measured and drawn. Peculiarly elongate tracks formed by bipedal dinosaurs walking flat-footed were found to be restricted to one end of the exposure. Sedimentological samples were collected to test for substrate differences that could account for this change in locomotor behavior. Several tracks were collected; others were cast in latex. A geologic section was taken at this site by WRD and FAJJr to compare with the section at Tait Bjerg measured by DVK and LBC. Access was impeded by 85% snow cover between Camp V and the locality; in order to minimize travel time between the two, a satellite camp was established at the locality on July 5th which accommodated Dr. Gatesy until July 12th.

Camp VI (29 June - 13 July; WWA, NHS, LBC, DVK): 71º 28.34' North, 22º 40.43' West, elevation 940 feet. An area encompassing the entirety of Tait Bjerg, bounded by Passagen to the south, Buch Bjerg to the north, and Carlsberg Fjord to the east, provides excellent exposures of the Malmros Klint and Ørsted Dal Members as well as the type locality for the Tait Bjerg beds at the summit of the mountain. Despite nearly 50% snow cover, paleontological prospecting was undertaken and a rich bone bed was discovered in the Malmros Klint Member on the west side of Tait Bjerg. This horizon appears to represent a somewhat more terrestrial component of tetrapods than that in other bone lenses previously sampled in 1989 and 1991; matrix samples were collected for laboratory analysis. Drs. Dennis V. Kent and Lars B. Clemmensen were able to complete a 220m paleomagnetic section encompassing the Malmros Klint - Ørsted Dal boundary, as well as collect data pertaining to sedimentary cyclicity; rock samples for use with other dating techniques were collected as well. The stratigraphic work was made difficult by the unfavorable snow conditions but nonetheless holds substantial promise for providing a geochronologic framework for the upper part of the Fleming Fjord Formation independant of the vertebrate fauna.

Camp IX (13 July - 31 July): 71º 50.416' North, 23º 39.281' West, elevation 2,400 feet. The rugged terrain of Sydkronen, bounded by Ørsted Dal to the south and Gipsdalen to the west, was discovered in 1991 to offer outstanding exposures of the Fleming Fjord Formation as well as the possibility of reconnaissance of Middle Triassic sediments to the west. Snow cover in this area was less than 15%. The principal discoveries included a nearly complete skull (Figure 6) and numerous postcranial elements of the aëtosaur *Aëtosaurus ferratus*; the specimen is important because this species is a useful geochronological indicator and its occurence in the upper part of the Fleming Fjord Formation is evidence that the Ørsted Dal and Malmros Klint Members are as least as old as mid-Norian, and perhaps older. The remains of a small theropod dinosaur (Figure 7 and 8) was this season's most unusual find; although trackways of theropods are common through the upper part of the Fleming Fjord Formation, skeletal evidence of theropods has proven in previous field seasons to be extremely rare and largely limited to isolated teeth. Drs. Kent and Clemmensen completed a staratigraphic section and sampled for paleomagnetic analysis to the extent permitted by the presence of red beds. Reconnaissance of the Middle and Lower Triassic proved disappointing; although the Gipsdalen and Pingo Dal Formations are well exposed in this area (Figure 7), careful surveys conducted by members of the expedition revealed no substantial prospects for further vertebrate paleontological study.

Camp X (31 July - 1 August): 71° 44.76'North, 23° 34.21'West, elevation 200 feet. This site in Ørsted Dal, near the confluence of Ørsted Dal and Pingo Dal, was selected as a landing strip for the Flugfelag Nordurlands Twin Otter that retrieved the expedition on August 1st.

D. SUMMARY OF FINDINGS TO DATE

As the result of this and the previous three expeditions to Jameson Land, the Fleming Fjord fauna is now known to include a substantial representation of European taxa, including prosauropod (*Plateosaurus*) and theropod dinosaurs, a turtle (*Proganochelys*), an aëtosaur (*Aëtosaurus ferratus*), a pterosaur (*Eudimorphodon*), plagiosaurid (*Gerrothorax*) and capitosauroid (cf. *Mastodonsaurus*) amphibians, as well as other taxa (a phytosaur, sharks, lungfish, and semionotids). The paleomagnetic samples collected offer the possibility of correlating the Triassic-Jurassic rocks of East Greenland with the well documented Newark Series, providing a more comprehensive synthesis of Late Triassic faunal evolution than has been possible before. The Fleming Fjord fauna is potentially a key biostratigraphic link between continental sediments of Europe and North America.

Although the specimens collected during the 1992 and previous field seasons require preparation before further study and detailed identifications can be made, it is already evident that the fauna of the Fleming Fjord Formation will be one of the best documented Late Triassic faunas known in the world. When the age of the Fleming Fjord fauna is more accurately established on the basis of detailed faunal comparisons and geomagnetic studies, a substantial contribution will be made to our understanding of those major faunal transitions that took place between Late Triassic and Early Jurassic time.

The first scientific publication based on the results of this project (entitled "Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland") is nearly completed and may be expected to appear in the Bulletin of the Geological Society of Denmark.

E. ACKNOWLEDGMENTS

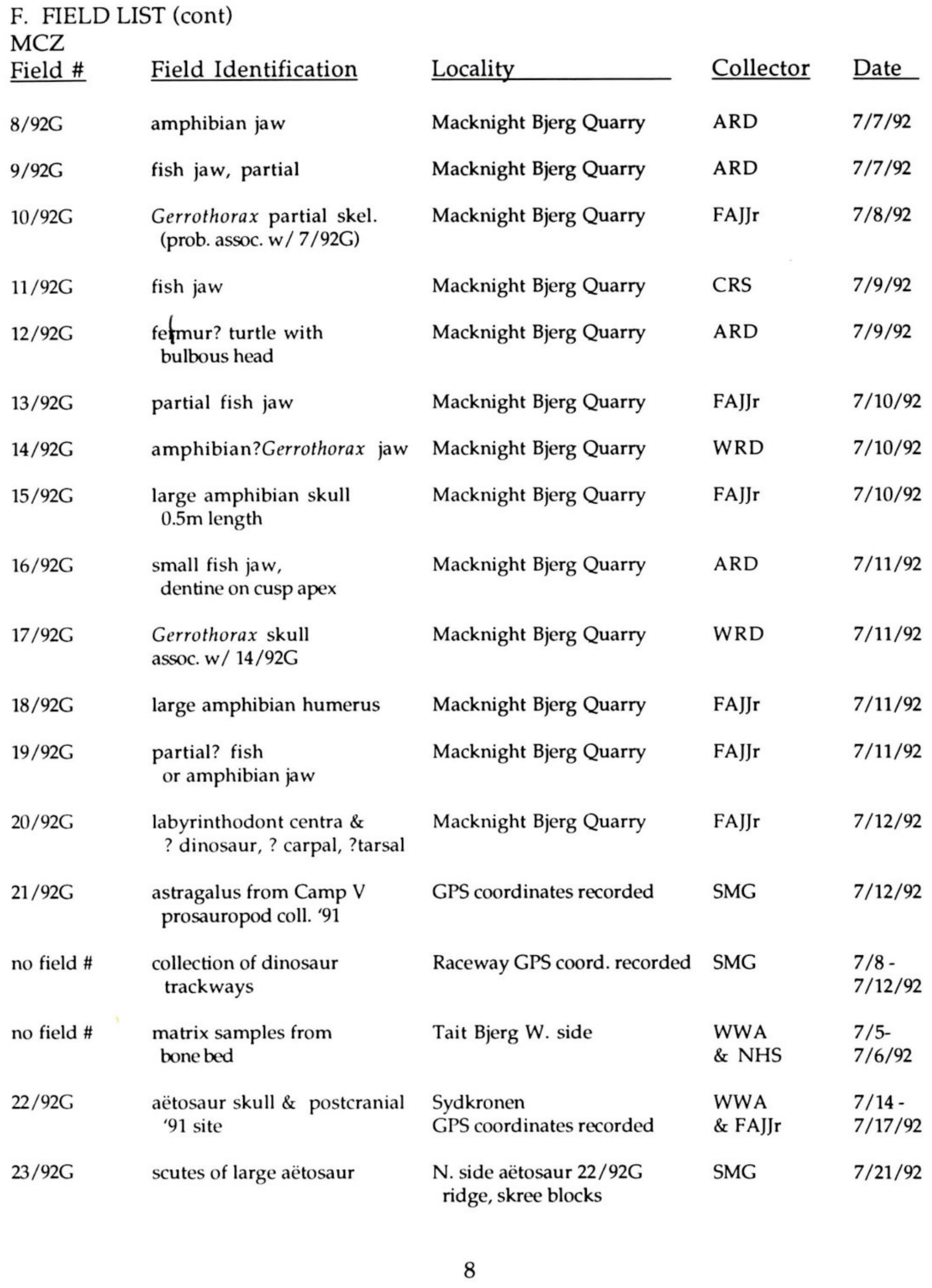
We are grateful to the National Science Foundation (Division of Earth Sciences, Geology and Paleontology Program), to the Museum of Comparative Zoology (Putnam Expedition Grant), and to the Commission for Scientific Research in Greenland for support of this project. We extend warmest thanks to the officers and personnel of Air Operations, U. S. Naval Air Station, Keflavik, Iceland, for their enthusiastic helpfulness in transferring personnel and cargo to and from Greenland,

and particularly wish to acknowledge Commander William E. Spencer, Master Chief Petty Officer David A. Johnson and Chief Petty Officer John C. Newman. We also wish to express our deep appreciation for the hospitality and logistical support of Else Sanko and Airport Chief Aka Lynge at Constable Pynt; through their good efforts a range of unexpected problems were gracefully overcome. As before, we are indebted to the management and flight personnel of GreenlandAir Charter A/S, and in particular to the skillful pilots, Messrs. Sturla Skoglund (who managed to get the expedition launched despite difficult conditions), T. Ardeholm (who ferried the move to Camp IX), and Håkon S. Kristensen (who extricated the expedition from the mountainous terrain of Sydkronen with memorable style). We sincerely thank the radio operators of AFIS, Messrs Hans Erik Jacobsen (28 June - 26 July) and Per Bendixen (27 July - 1 August), for providing essential communication services between Constable Pynt and our base camps, and for their patience with traffic broadcast in less than ideal conditions. Finally, but by no means least, we salute the management and flight personnel of Flugfelag Nordurlands, a flying company that can be counted on: Messrs. Fridjon Einarsson and Olafur M. Bertelsson (for logistical arrangments in Iceland), Captain Johann Skirnisson and First Officer Agust J. Magnusson, and the air operations manager, Captain Sigurdur Adalsteinsson, who managed a landing and takeoff on a short airstrip at Camp X which had been selected by expeditionary members who have never flown a plane.

F. FIELD LIST

The following preliminary identifications are based upon examination of specimens in the field, and may be revised when laboratory preparation and detailed studies are undertaken.

MCZ Field #	Field Identification	Locality	Collector	Date
1/92G	small fish Jaw with conical Teeth	Macknight Bjerg Quarry	FAJJr	7/1/92
2/92G	small jaw with bifurcated, cusped teeth	Macknight Bjerg Quarry	CRS	7/1/92
3/92G	*Gerrothorax* skull (in 3 blocks)	Macknight Bjerg Quarry	FAJJr & ARD	7/4/92
4/92G	isolated theropod tooth	Macknight Bjerg Quarry	WRD	7/4/92
5/92G	small bone accumulation (for lab exam)	Macknight Bjerg Quarry	WRD	7/4/92
6/92G	small jaw with serrated tooth	Macknight Bjerg Quarry	CRS	7/5/92
7/92G	partial skull *Gerrothorax*	Macknight Bjerg Quarry	FAJJr	7/5/92



F. FIELD LIST (cont)

MCZ Field #	Field Identification	Locality	Collector	Date
8/92G	amphibian jaw	Macknight Bjerg Quarry	ARD	7/7/92
9/92G	fish jaw, partial	Macknight Bjerg Quarry	ARD	7/7/92
10/92G	*Gerrothorax* partial skel. (prob. assoc. w/ 7/92G)	Macknight Bjerg Quarry	FAJJr	7/8/92
11/92G	fish jaw	Macknight Bjerg Quarry	CRS	7/9/92
12/92G	femur? turtle with bulbous head	Macknight Bjerg Quarry	ARD	7/9/92
13/92G	partial fish jaw	Macknight Bjerg Quarry	FAJJr	7/10/92
14/92G	amphibian?*Gerrothorax* jaw	Macknight Bjerg Quarry	WRD	7/10/92
15/92G	large amphibian skull 0.5m length	Macknight Bjerg Quarry	FAJJr	7/10/92
16/92G	small fish jaw, dentine on cusp apex	Macknight Bjerg Quarry	ARD	7/11/92
17/92G	*Gerrothorax* skull assoc. w/ 14/92G	Macknight Bjerg Quarry	WRD	7/11/92
18/92G	large amphibian humerus	Macknight Bjerg Quarry	FAJJr	7/11/92
19/92G	partial? fish or amphibian jaw	Macknight Bjerg Quarry	FAJJr	7/11/92
20/92G	labyrinthodont centra & ? dinosaur, ? carpal, ?tarsal	Macknight Bjerg Quarry	FAJJr	7/12/92
21/92G	astragalus from Camp V prosauropod coll. '91	GPS coordinates recorded	SMG	7/12/92
no field #	collection of dinosaur trackways	Raceway GPS coord. recorded	SMG	7/8 - 7/12/92
no field #	matrix samples from bone bed	Tait Bjerg W. side	WWA & NHS	7/5- 7/6/92
22/92G	aëtosaur skull & postcranial '91 site	Sydkronen GPS coordinates recorded	WWA & FAJJr	7/14 - 7/17/92
23/92G	scutes of large aëtosaur	N. side aëtosaur 22/92G ridge, skree blocks	SMG	7/21/92

F. FIELD LIST (cont)

MCZ Field #	Field Identification	Locality	Collector	Date
24/92G	small fish w/ scales and body outline	50 m. N.E. 22/92Gf	ARD	7/21/92
25/92G	trackways, short prints with claws	Ørsted Dal Member; W. side Sydkromen	SMG	7/28/92
26/92G	theropod partial skeleton	GPS coordinates recorded	WWA et al	7/27 - 7/28/92
27/92G	dinosaur tracks (2; 1 positive imprint)	Ørsted Dal Member	SMG	7/30/92
No field # 22/[illegible]	Reptile or fish? large jaw w/serrated teeth	Camp III Area Above Mammal layer	NHS	7/92

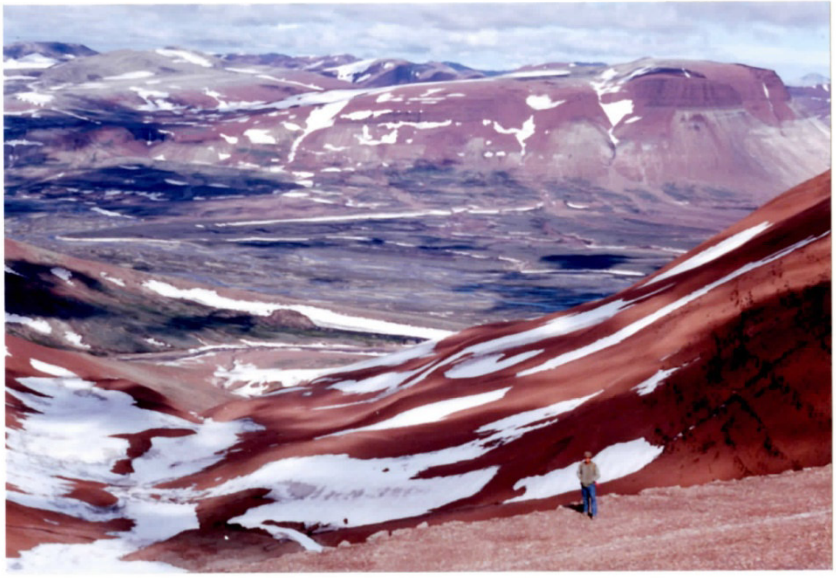


Fig. 1. Comparable views taken from the Raceway locality (71° 24.88' N, 22° 33.17' W) looking north to Tait Bjerg and Camp VI in 1991 (above) and 1992 (below). The substantial snow cover impeded this year's operations.

Fig. 2. Skull of a large labyrinthodont amphibian measuring 48cm. from end of snout (at the left; at the tip of the chisel) to the occiput. The orbits and characteristic patterning of the dermal bone are evident. This dorsal view was taken of the specimen *in situ* in the Macknight Bjerg Quarry.

Fig 3. Skull of the broad-headed amphibian *Gerrothorax*. This ventral view of the specimen, recovered from the Macknight Bjerg Quarry, was revealed through laboratory preparation at the MCZ by A. R. Davidson.

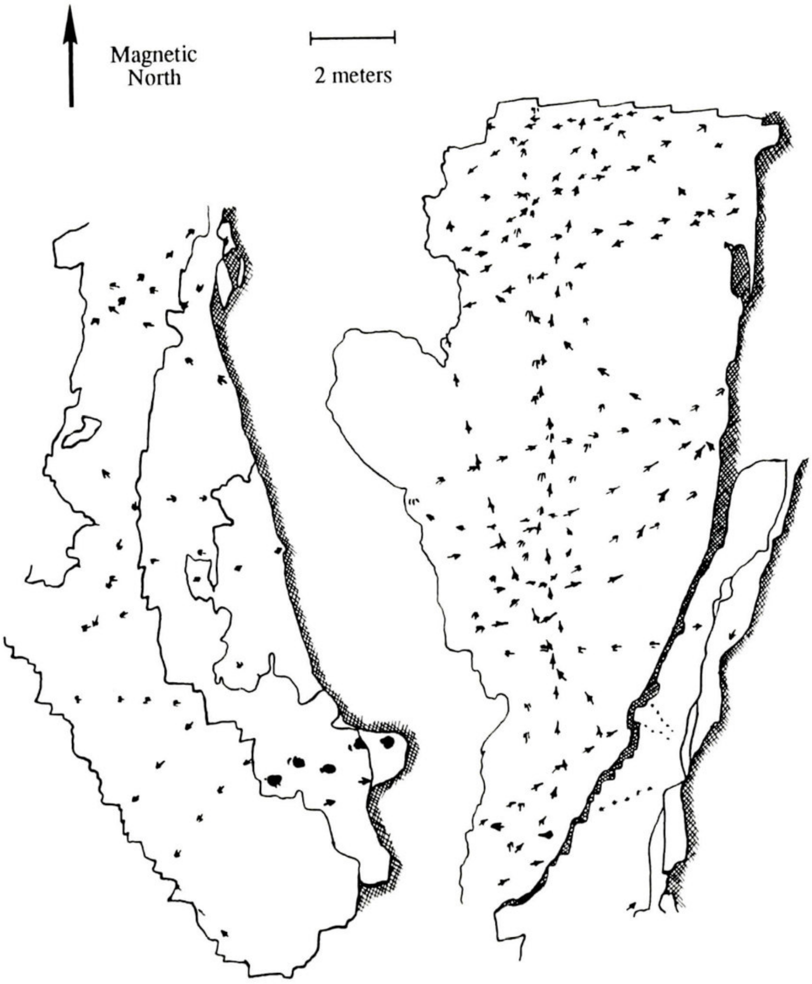


Fig 4. Dinosaur footprints exposed at the "Raceway" locality. Diagram prepared by Dr. S. M. Gatesy.

Fig 5. A large trackway, probably that of a prosauropod dinosaur, at the "Raceway" locality. For scale, the length of the marsh pick is 89 cm.

Fig 6. A partially prepared skull of *Aëtosaurus ferratus*, left lateral aspect. Initial preparation has exposed the left orbit as well as maxillary and mandibular teeth.

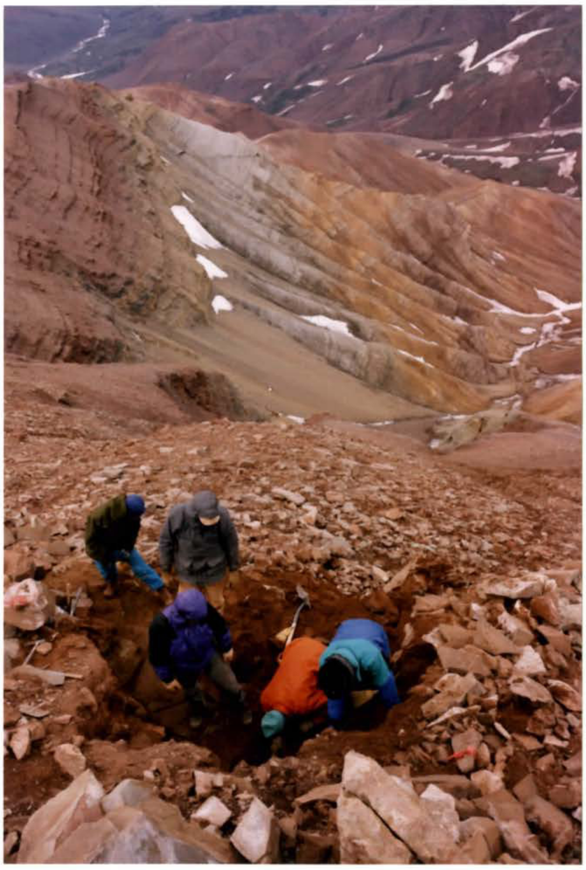
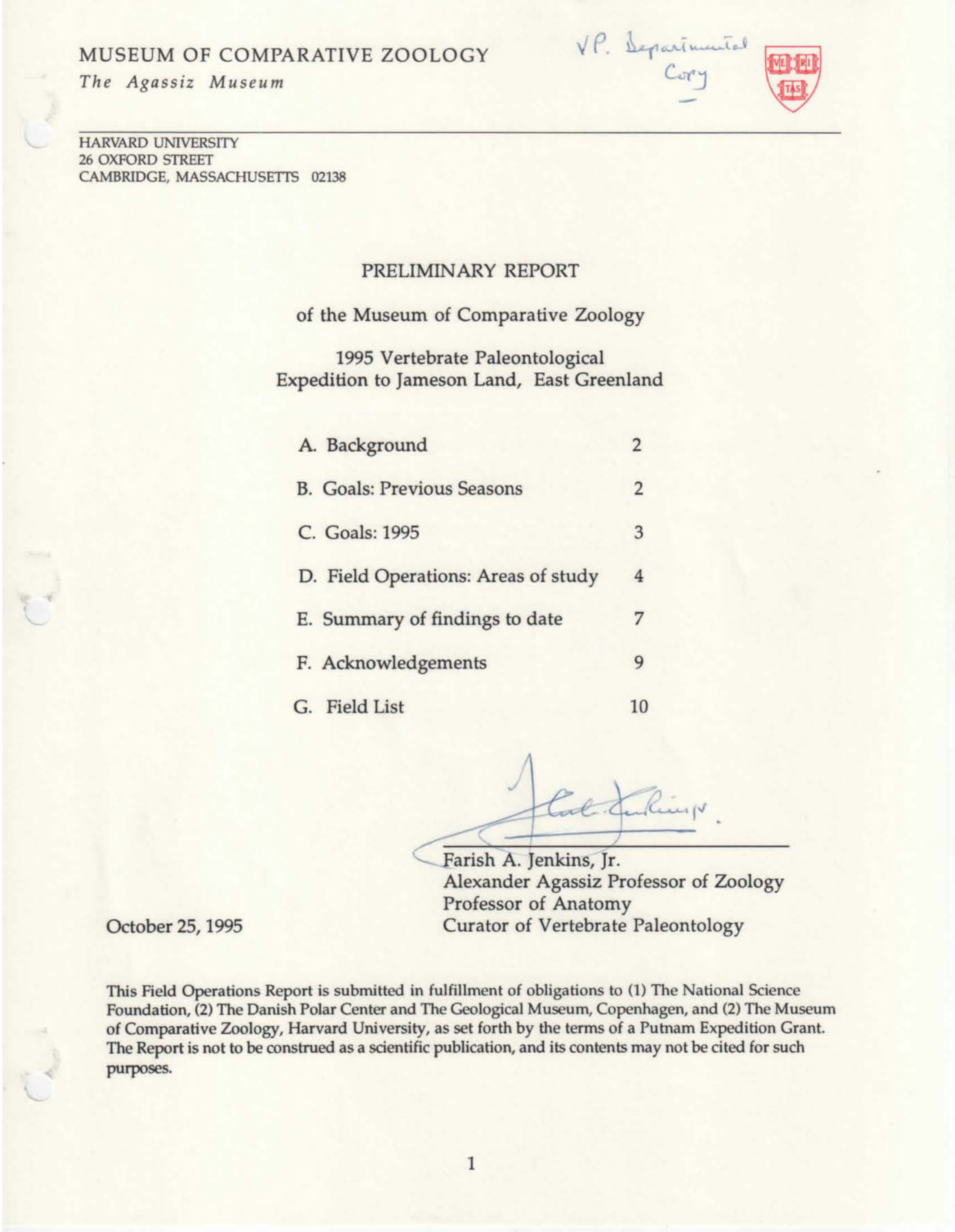


Fig 7. The theropod dinosaur locality on Sydkronen. Below the quarry is exposed a section of some 3,000 feet of Triassic sediments.

Fig 8. Postcranial skeletal elements of a theropod dinosaur, including femur, ribs and vertebrae.

A9 – Field report 1995 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1995 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



MUSEUM OF COMPARATIVE ZOOLOGY
The Agassiz Museum

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PRELIMINARY REPORT

of the Museum of Comparative Zoology

1995 Vertebrate Paleontological
Expedition to Jameson Land, East Greenland

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Farish A. Jenkins, Jr.
Alexander Agassiz Professor of Zoology
Professor of Anatomy
Curator of Vertebrate Paleontology

October 25, 1995

This Field Operations Report is submitted in fulfillment of obligations to (1) The National Science Foundation, (2) The Danish Polar Center and The Geological Museum, Copenhagen, and (2) The Museum of Comparative Zoology, Harvard University, as set forth by the terms of a Putnam Expedition Grant. The Report is not to be construed as a scientific publication, and its contents may not be cited for such purposes.

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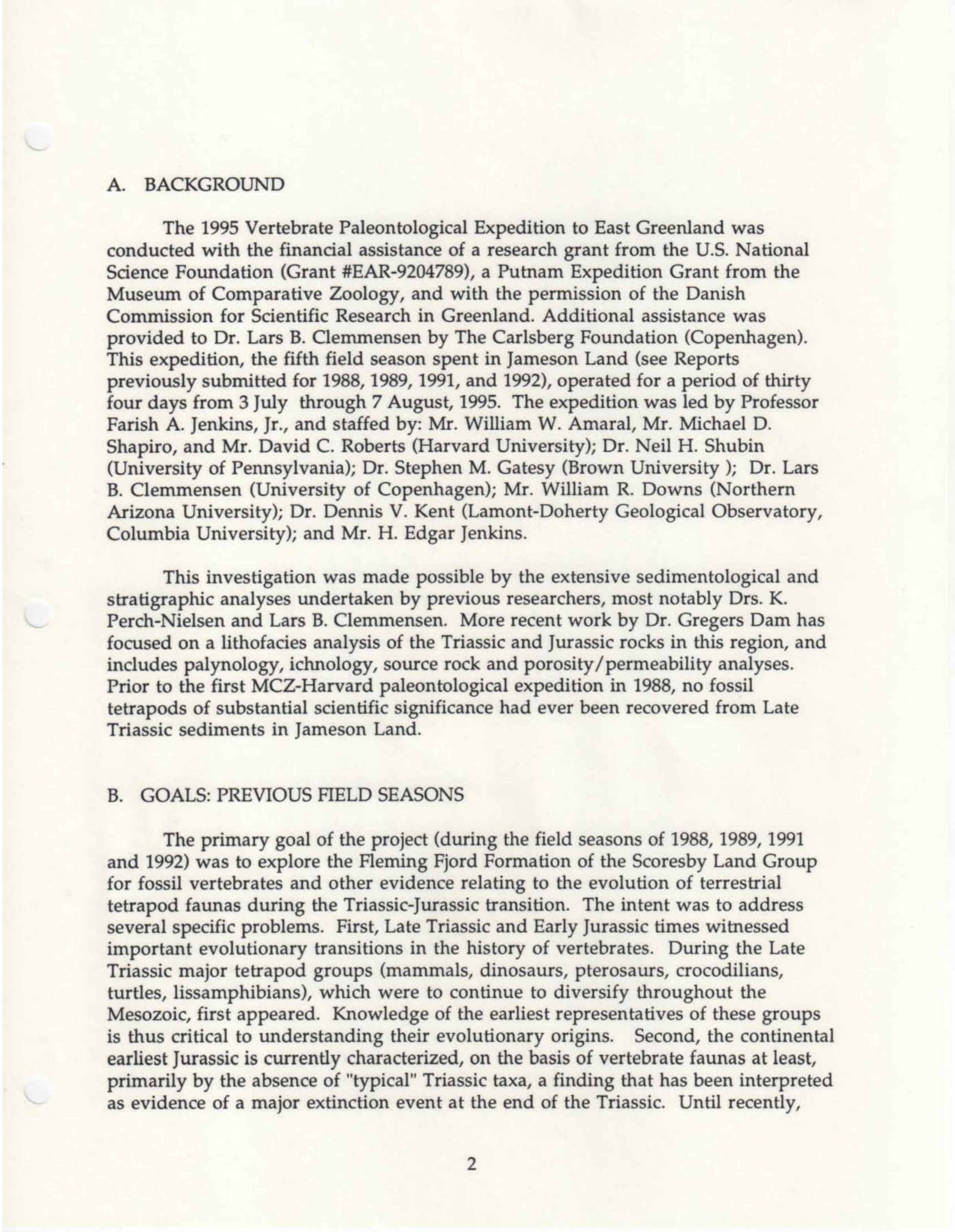


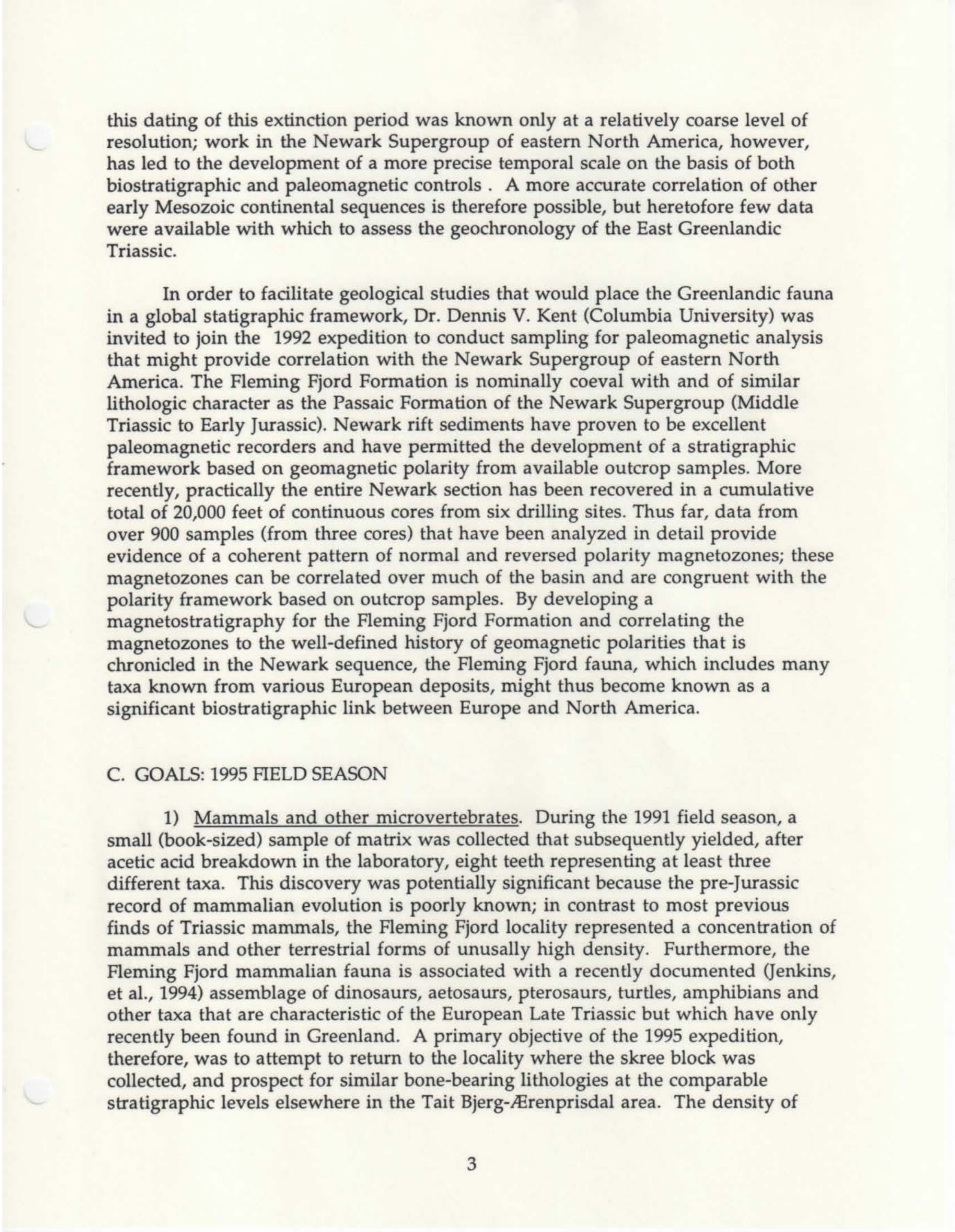
A. BACKGROUND

The 1995 Vertebrate Paleontological Expedition to East Greenland was conducted with the financial assistance of a research grant from the U.S. National Science Foundation (Grant #EAR-9204789), a Putnam Expedition Grant from the Museum of Comparative Zoology, and with the permission of the Danish Commission for Scientific Research in Greenland. Additional assistance was provided to Dr. Lars B. Clemmensen by The Carlsberg Foundation (Copenhagen). This expedition, the fifth field season spent in Jameson Land (see Reports previously submitted for 1988, 1989, 1991, and 1992), operated for a period of thirty four days from 3 July through 7 August, 1995. The expedition was led by Professor Farish A. Jenkins, Jr., and staffed by: Mr. William W. Amaral, Mr. Michael D. Shapiro, and Mr. David C. Roberts (Harvard University); Dr. Neil H. Shubin (University of Pennsylvania); Dr. Stephen M. Gatesy (Brown University); Dr. Lars B. Clemmensen (University of Copenhagen); Mr. William R. Downs (Northern Arizona University); Dr. Dennis V. Kent (Lamont-Doherty Geological Observatory, Columbia University); and Mr. H. Edgar Jenkins.

This investigation was made possible by the extensive sedimentological and stratigraphic analyses undertaken by previous researchers, most notably Drs. K. Perch-Nielsen and Lars B. Clemmensen. More recent work by Dr. Gregers Dam has focused on a lithofacies analysis of the Triassic and Jurassic rocks in this region, and includes palynology, ichnology, source rock and porosity/permeability analyses. Prior to the first MCZ-Harvard paleontological expedition in 1988, no fossil tetrapods of substantial scientific significance had ever been recovered from Late Triassic sediments in Jameson Land.

B. GOALS: PREVIOUS FIELD SEASONS

The primary goal of the project (during the field seasons of 1988, 1989, 1991 and 1992) 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 address several specific 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, lissamphibians), 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. Second, the continental earliest Jurassic is currently characterized, on the 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. Until recently,

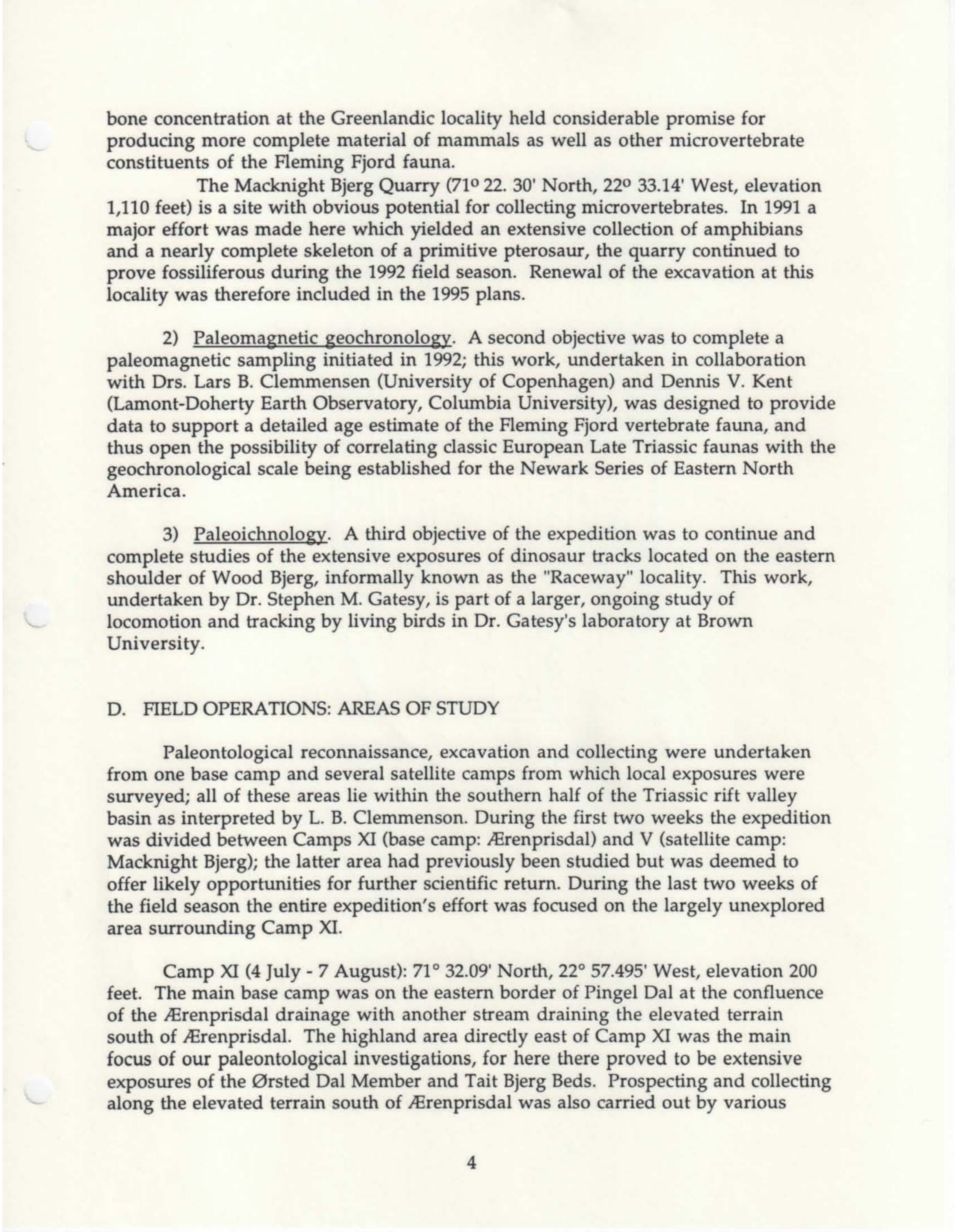


this dating of this extinction period was known only at a relatively coarse level of resolution; work in the Newark Supergroup of eastern North America, however, has led to the development of a more precise temporal scale on the basis of both biostratigraphic and paleomagnetic controls . A more accurate correlation of other early Mesozoic continental sequences is therefore possible, but heretofore few data were available with which to assess the geochronology of the East Greenlandic Triassic.

In order to facilitate geological studies that would place the Greenlandic fauna in a global statigraphic framework, Dr. Dennis V. Kent (Columbia University) was invited to join the 1992 expedition to conduct sampling for paleomagnetic analysis that might provide correlation with the Newark Supergroup of eastern North America. The Fleming Fjord Formation is nominally coeval with and of similar lithologic character as the Passaic Formation of the Newark Supergroup (Middle Triassic to Early Jurassic). Newark rift sediments have proven to be excellent paleomagnetic recorders and have permitted the development of a stratigraphic framework based on geomagnetic polarity from available outcrop samples. More recently, practically the entire Newark section has been recovered in a cumulative total of 20,000 feet of continuous cores from six drilling sites. Thus far, data from over 900 samples (from three cores) that have been analyzed in detail provide evidence of a coherent pattern of normal and reversed polarity magnetozones; these magnetozones can be correlated over much of the basin and are congruent with the polarity framework based on outcrop samples. By developing a magnetostratigraphy for the Fleming Fjord Formation and correlating the magnetozones to the well-defined history of geomagnetic polarities that is chronicled in the Newark sequence, the Fleming Fjord fauna, which includes many taxa known from various European deposits, might thus become known as a significant biostratigraphic link between Europe and North America.

C. GOALS: 1995 FIELD SEASON

1) Mammals and other microvertebrates. During the 1991 field season, a small (book-sized) sample of matrix was collected that subsequently yielded, after acetic acid breakdown in the laboratory, eight teeth representing at least three different taxa. This discovery was potentially significant because the pre-Jurassic record of mammalian evolution is poorly known; in contrast to most previous finds of Triassic mammals, the Fleming Fjord locality represented a concentration of mammals and other terrestrial forms of unusally high density. Furthermore, the Fleming Fjord mammalian fauna is associated with a recently documented (Jenkins, et al., 1994) assemblage of dinosaurs, aetosaurs, pterosaurs, turtles, amphibians and other taxa that are characteristic of the European Late Triassic but which have only recently been found in Greenland. A primary objective of the 1995 expedition, therefore, was to attempt to return to the locality where the skree block was collected, and prospect for similar bone-bearing lithologies at the comparable stratigraphic levels elsewhere in the Tait Bjerg-Ærenprisdal area. The density of



bone concentration at the Greenlandic locality held considerable promise for producing more complete material of mammals as well as other microvertebrate constituents of the Fleming Fjord fauna.

The Macknight Bjerg Quarry (71º 22. 30' North, 22º 33.14' West, elevation 1,110 feet) is a site with obvious potential for collecting microvertebrates. In 1991 a major effort was made here which yielded an extensive collection of amphibians and a nearly complete skeleton of a primitive pterosaur, the quarry continued to prove fossiliferous during the 1992 field season. Renewal of the excavation at this locality was therefore included in the 1995 plans.

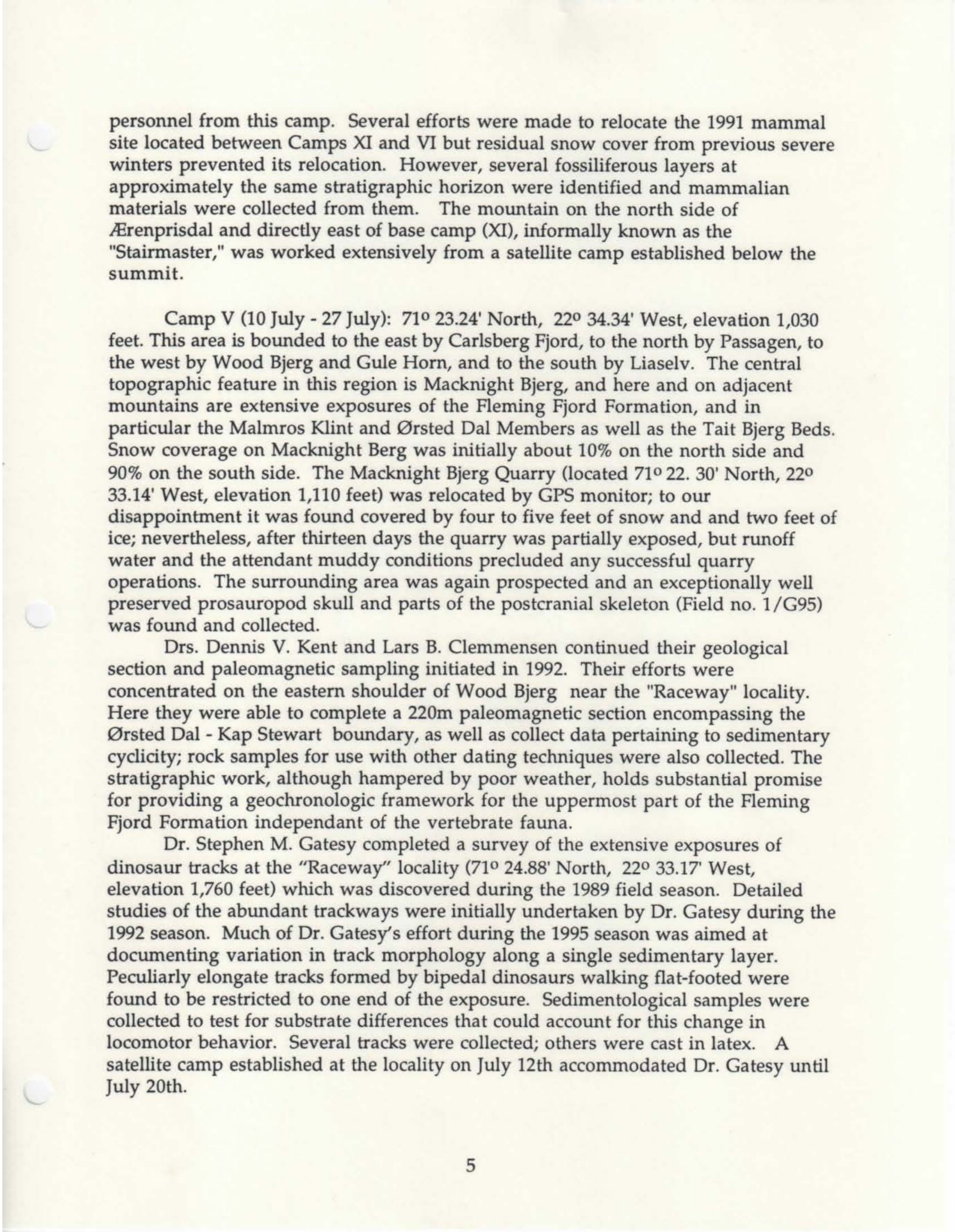
2) Paleomagnetic geochronology. A second objective was to complete a paleomagnetic sampling initiated in 1992; this work, undertaken in collaboration with Drs. Lars B. Clemmensen (University of Copenhagen) and Dennis V. Kent (Lamont-Doherty Earth Observatory, Columbia University), was designed to provide data to support a detailed age estimate of the Fleming Fjord vertebrate fauna, and thus open the possibility of correlating classic European Late Triassic faunas with the geochronological scale being established for the Newark Series of Eastern North America.

3) Paleoichnology. A third objective of the expedition was to continue and complete studies of the extensive exposures of dinosaur tracks located on the eastern shoulder of Wood Bjerg, informally known as the "Raceway" locality. This work, undertaken by Dr. Stephen M. Gatesy, is part of a larger, ongoing study of locomotion and tracking by living birds in Dr. Gatesy's laboratory at Brown University.

D. FIELD OPERATIONS: AREAS OF STUDY

Paleontological reconnaissance, excavation and collecting were undertaken from one base camp and several satellite camps from which local exposures were surveyed; all of these areas lie within the southern half of the Triassic rift valley basin as interpreted by L. B. Clemmenson. During the first two weeks the expedition was divided between Camps XI (base camp: Ærenprisdal) and V (satellite camp: Macknight Bjerg); the latter area had previously been studied but was deemed to offer likely opportunities for further scientific return. During the last two weeks of the field season the entire expedition's effort was focused on the largely unexplored area surrounding Camp XI.

Camp XI (4 July - 7 August): 71° 32.09' North, 22° 57.495' West, elevation 200 feet. The main base camp was on the eastern border of Pingel Dal at the confluence of the Ærenprisdal drainage with another stream draining the elevated terrain south of Ærenprisdal. The highland area directly east of Camp XI was the main focus of our paleontological investigations, for here there proved to be extensive exposures of the Ørsted Dal Member and Tait Bjerg Beds. Prospecting and collecting along the elevated terrain south of Ærenprisdal was also carried out by various

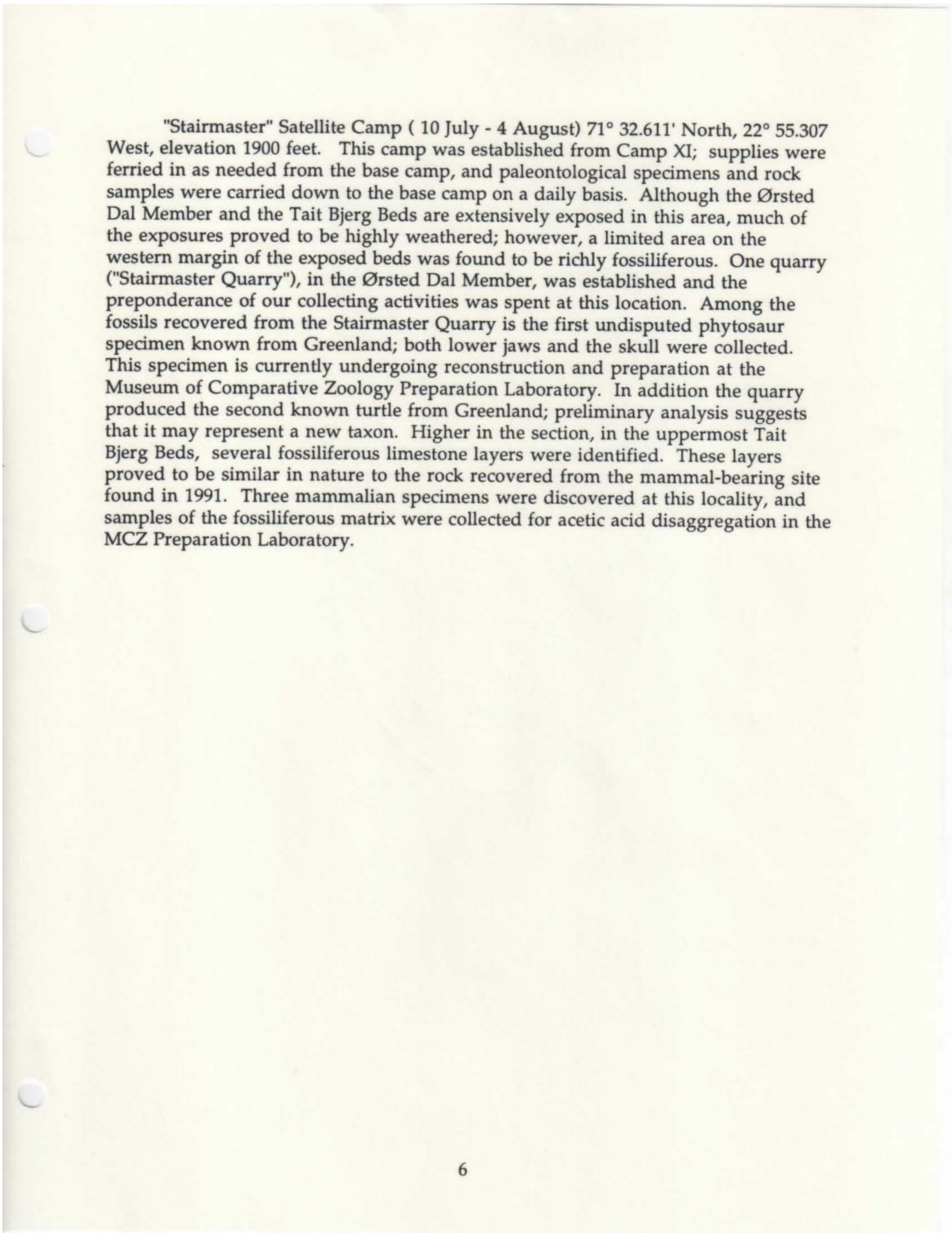


personnel from this camp. Several efforts were made to relocate the 1991 mammal site located between Camps XI and VI but residual snow cover from previous severe winters prevented its relocation. However, several fossiliferous layers at approximately the same stratigraphic horizon were identified and mammalian materials were collected from them. The mountain on the north side of Ærenprisdal and directly east of base camp (XI), informally known as the "Stairmaster," was worked extensively from a satellite camp established below the summit.

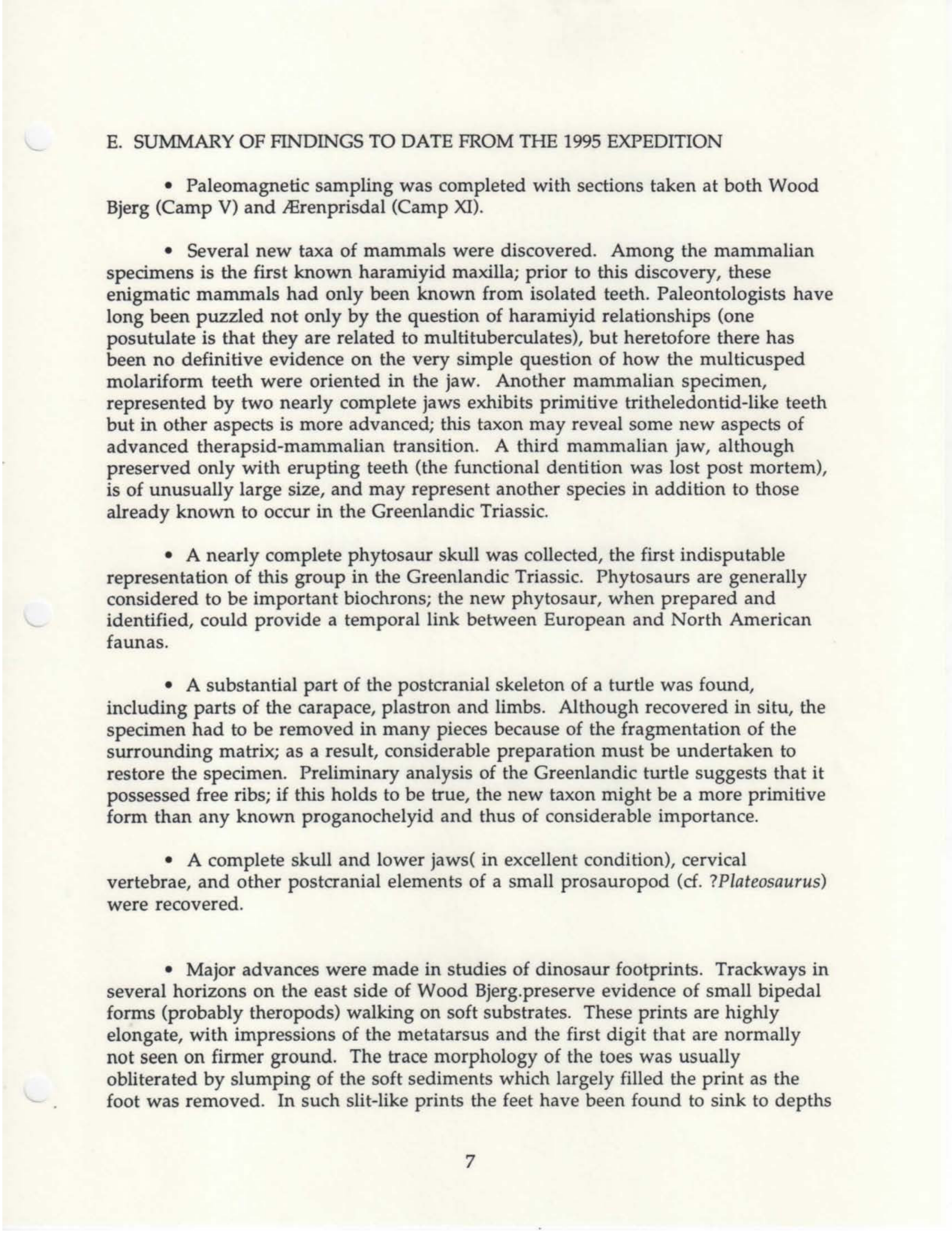
Camp V (10 July - 27 July): 71° 23.24' North, 22° 34.34' West, elevation 1,030 feet. This area is bounded to the east by Carlsberg Fjord, to the north by Passagen, to the west by Wood Bjerg and Gule Horn, and to the south by Liaselv. The central topographic feature in this region is Macknight Bjerg, and here and on adjacent mountains are extensive exposures of the Fleming Fjord Formation, and in particular the Malmros Klint and Ørsted Dal Members as well as the Tait Bjerg Beds. Snow coverage on Macknight Berg was initially about 10% on the north side and 90% on the south side. The Macknight Bjerg Quarry (located 71° 22. 30' North, 22° 33.14' West, elevation 1,110 feet) was relocated by GPS monitor; to our disappointment it was found covered by four to five feet of snow and and two feet of ice; nevertheless, after thirteen days the quarry was partially exposed, but runoff water and the attendant muddy conditions precluded any successful quarry operations. The surrounding area was again prospected and an exceptionally well preserved prosauropod skull and parts of the postcranial skeleton (Field no. 1/G95) was found and collected.

Drs. Dennis V. Kent and Lars B. Clemmensen continued their geological section and paleomagnetic sampling initiated in 1992. Their efforts were concentrated on the eastern shoulder of Wood Bjerg near the "Raceway" locality. Here they were able to complete a 220m paleomagnetic section encompassing the Ørsted Dal - Kap Stewart boundary, as well as collect data pertaining to sedimentary cyclicity; rock samples for use with other dating techniques were also collected. The stratigraphic work, although hampered by poor weather, holds substantial promise for providing a geochronologic framework for the uppermost part of the Fleming Fjord Formation independant of the vertebrate fauna.

Dr. Stephen M. Gatesy completed a survey of the extensive exposures of dinosaur tracks at the "Raceway" locality (71° 24.88' North, 22° 33.17' West, elevation 1,760 feet) which was discovered during the 1989 field season. Detailed studies of the abundant trackways were initially undertaken by Dr. Gatesy during the 1992 season. Much of Dr. Gatesy's effort during the 1995 season was aimed at documenting variation in track morphology along a single sedimentary layer. Peculiarly elongate tracks formed by bipedal dinosaurs walking flat-footed were found to be restricted to one end of the exposure. Sedimentological samples were collected to test for substrate differences that could account for this change in locomotor behavior. Several tracks were collected; others were cast in latex. A satellite camp established at the locality on July 12th accommodated Dr. Gatesy until July 20th.



"Stairmaster" Satellite Camp (10 July - 4 August) 71° 32.611' North, 22° 55.307 West, elevation 1900 feet. This camp was established from Camp XI; supplies were ferried in as needed from the base camp, and paleontological specimens and rock samples were carried down to the base camp on a daily basis. Although the Ørsted Dal Member and the Tait Bjerg Beds are extensively exposed in this area, much of the exposures proved to be highly weathered; however, a limited area on the western margin of the exposed beds was found to be richly fossiliferous. One quarry ("Stairmaster Quarry"), in the Ørsted Dal Member, was established and the preponderance of our collecting activities was spent at this location. Among the fossils recovered from the Stairmaster Quarry is the first undisputed phytosaur specimen known from Greenland; both lower jaws and the skull were collected. This specimen is currently undergoing reconstruction and preparation at the Museum of Comparative Zoology Preparation Laboratory. In addition the quarry produced the second known turtle from Greenland; preliminary analysis suggests that it may represent a new taxon. Higher in the section, in the uppermost Tait Bjerg Beds, several fossiliferous limestone layers were identified. These layers proved to be similar in nature to the rock recovered from the mammal-bearing site found in 1991. Three mammalian specimens were discovered at this locality, and samples of the fossiliferous matrix were collected for acetic acid disaggregation in the MCZ Preparation Laboratory.



E. SUMMARY OF FINDINGS TO DATE FROM THE 1995 EXPEDITION

- Paleomagnetic sampling was completed with sections taken at both Wood Bjerg (Camp V) and Ærenprisdal (Camp XI).

- Several new taxa of mammals were discovered. Among the mammalian specimens is the first known haramiyid maxilla; prior to this discovery, these enigmatic mammals had only been known from isolated teeth. Paleontologists have long been puzzled not only by the question of haramiyid relationships (one posutulate is that they are related to multituberculates), but heretofore there has been no definitive evidence on the very simple question of how the multicusped molariform teeth were oriented in the jaw. Another mammalian specimen, represented by two nearly complete jaws exhibits primitive tritheledontid-like teeth but in other aspects is more advanced; this taxon may reveal some new aspects of advanced therapsid-mammalian transition. A third mammalian jaw, although preserved only with erupting teeth (the functional dentition was lost post mortem), is of unusually large size, and may represent another species in addition to those already known to occur in the Greenlandic Triassic.

- A nearly complete phytosaur skull was collected, the first indisputable representation of this group in the Greenlandic Triassic. Phytosaurs are generally considered to be important biochrons; the new phytosaur, when prepared and identified, could provide a temporal link between European and North American faunas.

- A substantial part of the postcranial skeleton of a turtle was found, including parts of the carapace, plastron and limbs. Although recovered in situ, the specimen had to be removed in many pieces because of the fragmentation of the surrounding matrix; as a result, considerable preparation must be undertaken to restore the specimen. Preliminary analysis of the Greenlandic turtle suggests that it possessed free ribs; if this holds to be true, the new taxon might be a more primitive form than any known proganochelyid and thus of considerable importance.

- A complete skull and lower jaws(in excellent condition), cervical vertebrae, and other postcranial elements of a small prosauropod (cf. ?*Plateosaurus*) were recovered.

- Major advances were made in studies of dinosaur footprints. Trackways in several horizons on the east side of Wood Bjerg.preserve evidence of small bipedal forms (probably theropods) walking on soft substrates. These prints are highly elongate, with impressions of the metatarsus and the first digit that are normally not seen on firmer ground. The trace morphology of the toes was usually obliterated by slumping of the soft sediments which largely filled the print as the foot was removed. In such slit-like prints the feet have been found to sink to depths of up to 15 cm. Based on experiments using living birds walking through deep mud, it was hypothesized that deep tracks should preserve the passage of the dinosaurs' toes in three dimensions. Preparation of footprints in the field confirmed the possibility of reconstructing sub-surface toe trajectories from such trackways, which has important implications for the understanding of dinosaur limb function during locomotion. Several large, deep prints were collected for analysis in the lab, along with more shallow prints preserving skin impressions. Observations made during the 1995 field season suggest that a spectrum of track shapes can be produced by the same animal and should not be construed as evidence for multiple species. Impressions left on the surface after the foot's passage may differ dramatically from the shape of the foot. Therefore, the morphological variation in bipedal footprints found in the Fleming Fjord Formation and at other sites of this age may be a consequence of substrate conditions rather than faunal or locomotor diversity.

•Summary. The 1995 field season produced major additions to the diverse assemblage of fossil vertebrates already known[1] from 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 a number of new species of mammals as well as prosauropod (*Plateosaurus*) and theropod dinosaurs, turtles (cf. *Proganochelys* and possibly another, new taxon), pterosaurs, aetosaurs (*Aetosaurus ferratus*, *Paratypothorax andressi*), phytosaurs, 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; a comparable age estimate for the underlying Malmros Klint Member cannot be made on the basis of the fauna as presently known but is expected to be substantiated by paleomagnetic data.

The quality and scientific importance of specimens discovered this year, particularly the mammalian taxa, warrant consideration for renewed expeditionary field work in Jameson Land in the near future. The field phase of our program therefore cannot yet be considered to be completed.

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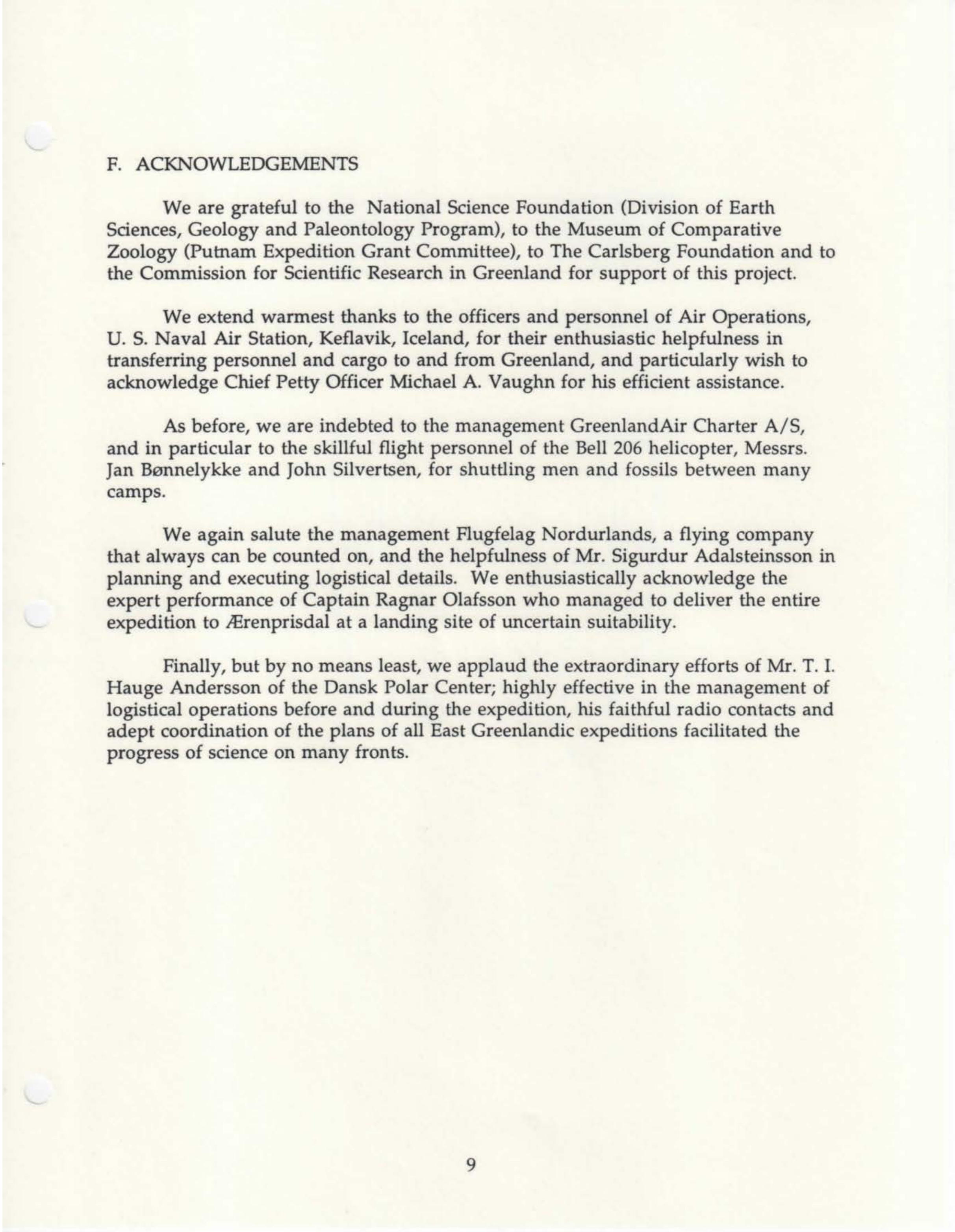
[1] See: F. A. Jenkins, Jr., N. H. Shubin, W. W. Amaral, S. M. Gatesy, C. R. Schaff, L. B. Clemmensen, W. R. Downs, A. R. Davidson, N. Bonde and F. Osbæck. 1994. *Late Triassic Continental Vertebrates and Depositional Environments of the Fleming Fjord Formation, Jameson Land, East Greenland.* Meddelelser om Grønland, Geoscience 32: 1 - 25, 17 figures.



F. ACKNOWLEDGEMENTS

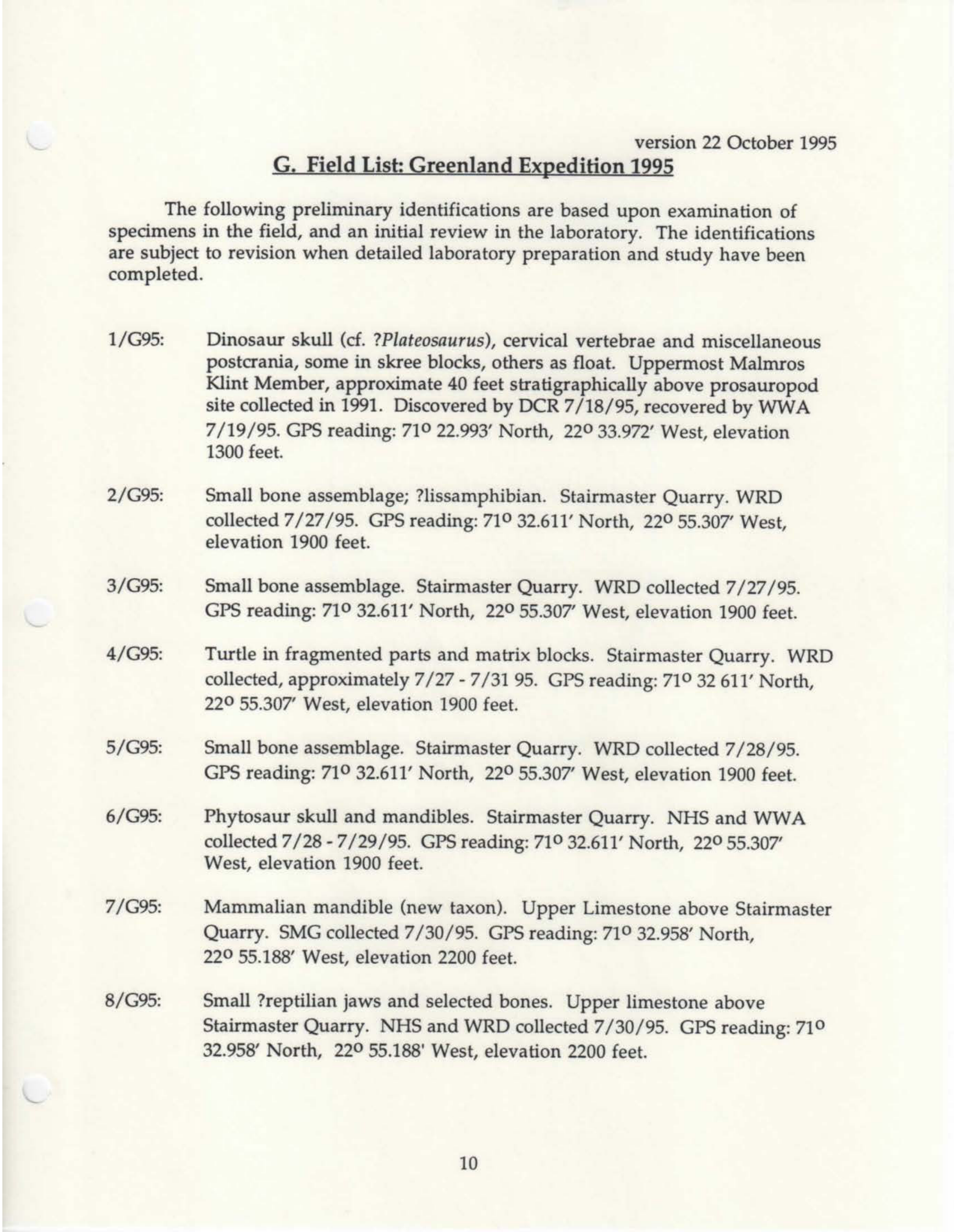
We are grateful to the National Science Foundation (Division of Earth Sciences, Geology and Paleontology Program), to the Museum of Comparative Zoology (Putnam Expedition Grant Committee), to The Carlsberg Foundation and to the Commission for Scientific Research in Greenland for support of this project.

We extend warmest thanks to the officers and personnel of Air Operations, U. S. Naval Air Station, Keflavik, Iceland, for their enthusiastic helpfulness in transferring personnel and cargo to and from Greenland, and particularly wish to acknowledge Chief Petty Officer Michael A. Vaughn for his efficient assistance.

As before, we are indebted to the management GreenlandAir Charter A/S, and in particular to the skillful flight personnel of the Bell 206 helicopter, Messrs. Jan Bønnelykke and John Silvertsen, for shuttling men and fossils between many camps.

We again salute the management Flugfelag Nordurlands, a flying company that always can be counted on, and the helpfulness of Mr. Sigurdur Adalsteinsson in planning and executing logistical details. We enthusiastically acknowledge the expert performance of Captain Ragnar Olafsson who managed to deliver the entire expedition to Ærenprisdal at a landing site of uncertain suitability.

Finally, but by no means least, we applaud the extraordinary efforts of Mr. T. I. Hauge Andersson of the Dansk Polar Center; highly effective in the management of logistical operations before and during the expedition, his faithful radio contacts and adept coordination of the plans of all East Greenlandic expeditions facilitated the progress of science on many fronts.



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G. Field List: Greenland Expedition 1995

The following preliminary identifications are based upon examination of specimens in the field, and an initial review in the laboratory. The identifications are subject to revision when detailed laboratory preparation and study have been completed.

1/G95: Dinosaur skull (cf. ?*Plateosaurus*), cervical vertebrae and miscellaneous postcrania, some in skree blocks, others as float. Uppermost Malmros Klint Member, approximate 40 feet stratigraphically above prosauropod site collected in 1991. Discovered by DCR 7/18/95, recovered by WWA 7/19/95. GPS reading: 71° 22.993′ North, 22° 33.972′ West, elevation 1300 feet.

2/G95: Small bone assemblage; ?lissamphibian. Stairmaster Quarry. WRD collected 7/27/95. GPS reading: 71° 32.611′ North, 22° 55.307′ West, elevation 1900 feet.

3/G95: Small bone assemblage. Stairmaster Quarry. WRD collected 7/27/95. GPS reading: 71° 32.611′ North, 22° 55.307′ West, elevation 1900 feet.

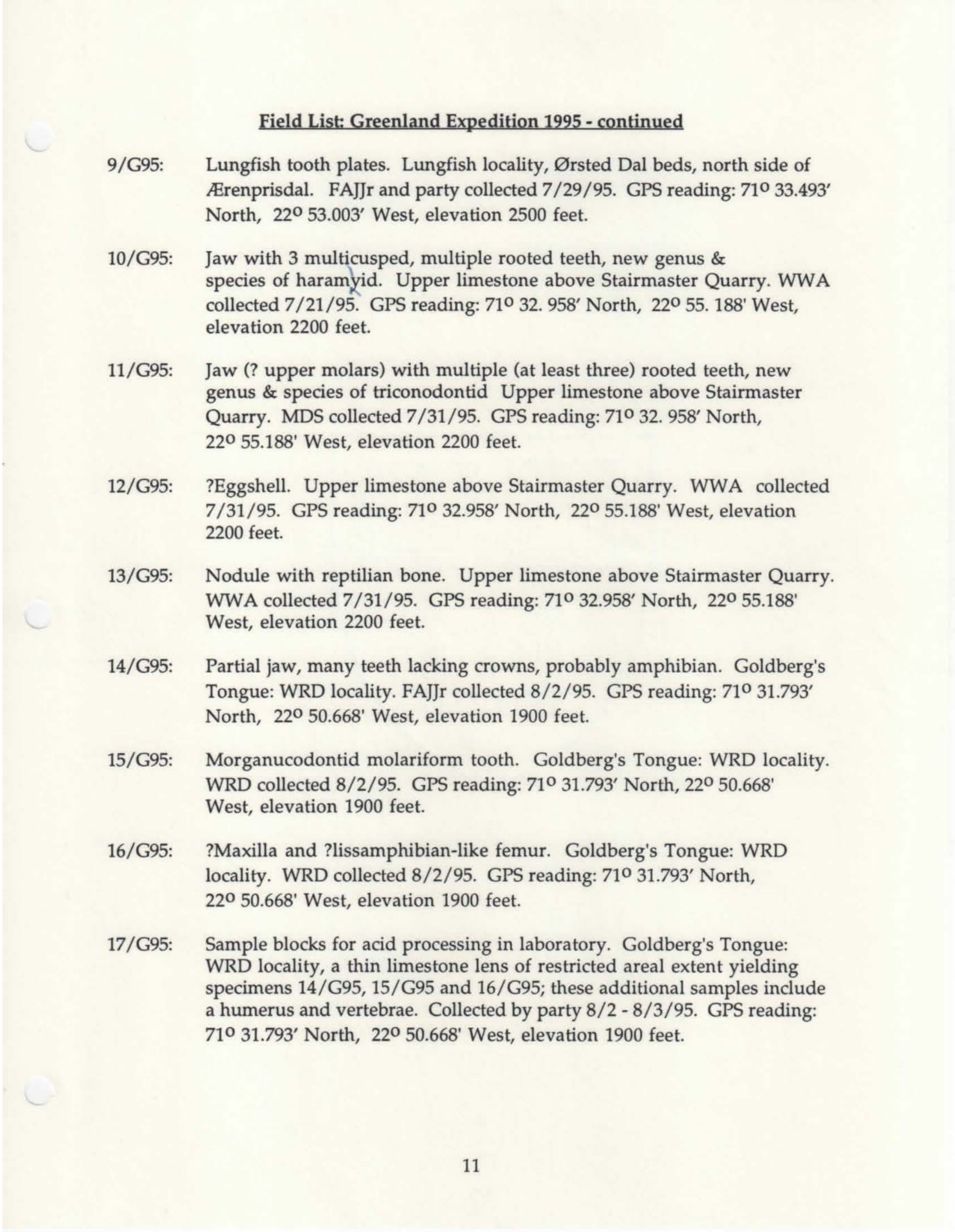
4/G95: Turtle in fragmented parts and matrix blocks. Stairmaster Quarry. WRD collected, approximately 7/27 - 7/31 95. GPS reading: 71° 32 611′ North, 22° 55.307′ West, elevation 1900 feet.

5/G95: Small bone assemblage. Stairmaster Quarry. WRD collected 7/28/95. GPS reading: 71° 32.611′ North, 22° 55.307′ West, elevation 1900 feet.

6/G95: Phytosaur skull and mandibles. Stairmaster Quarry. NHS and WWA collected 7/28 - 7/29/95. GPS reading: 71° 32.611′ North, 22° 55.307′ West, elevation 1900 feet.

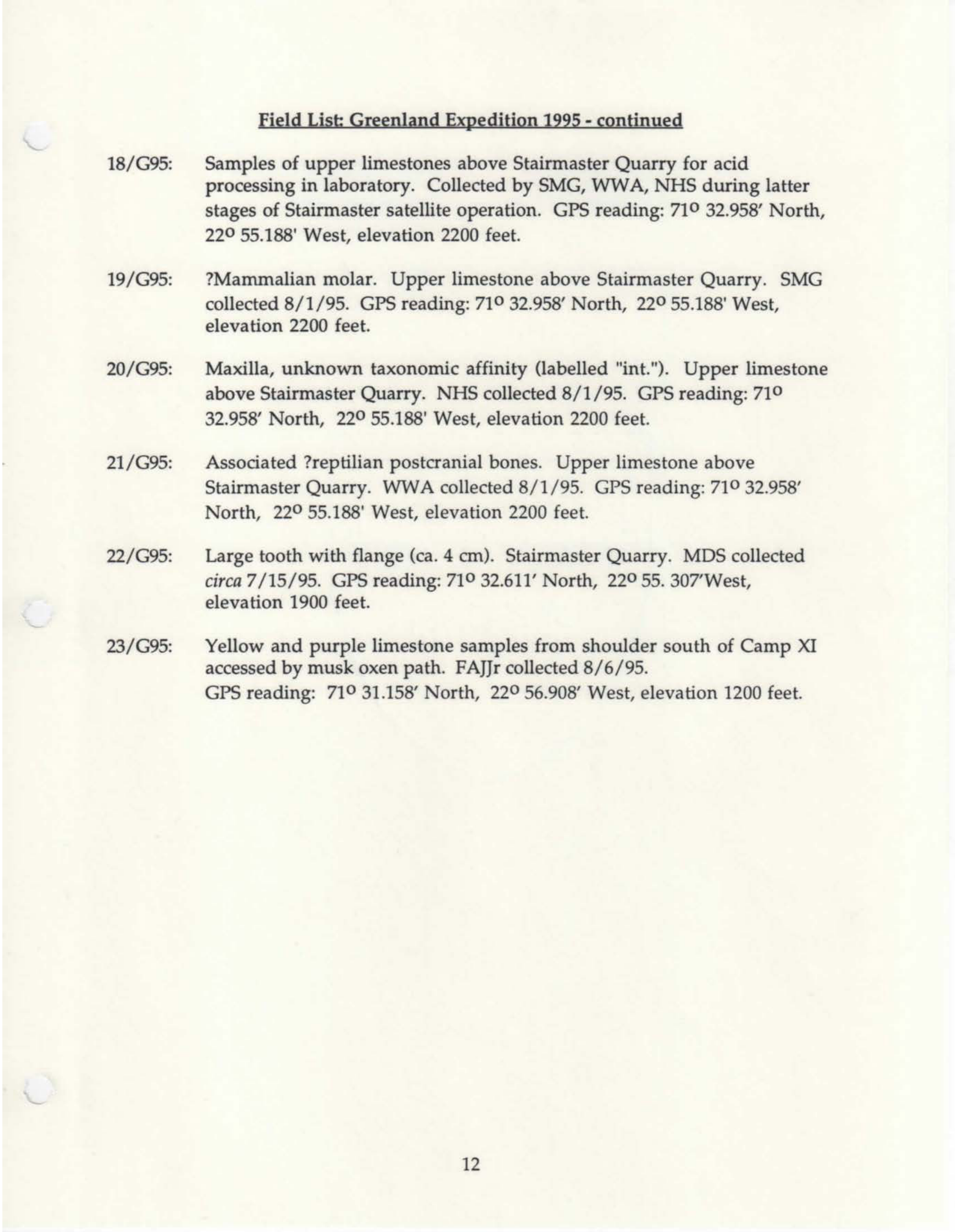
7/G95: Mammalian mandible (new taxon). Upper Limestone above Stairmaster Quarry. SMG collected 7/30/95. GPS reading: 71° 32.958′ North, 22° 55.188′ West, elevation 2200 feet.

8/G95: Small ?reptilian jaws and selected bones. Upper limestone above Stairmaster Quarry. NHS and WRD collected 7/30/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.



Field List: Greenland Expedition 1995 - continued

9/G95:	Lungfish tooth plates. Lungfish locality, Ørsted Dal beds, north side of Ærenprisdal. FAJJr and party collected 7/29/95. GPS reading: 71° 33.493′ North, 22° 53.003′ West, elevation 2500 feet.
10/G95:	Jaw with 3 multicusped, multiple rooted teeth, new genus & species of haramyid. Upper limestone above Stairmaster Quarry. WWA collected 7/21/95. GPS reading: 71° 32. 958′ North, 22° 55. 188' West, elevation 2200 feet.
11/G95:	Jaw (? upper molars) with multiple (at least three) rooted teeth, new genus & species of triconodontid Upper limestone above Stairmaster Quarry. MDS collected 7/31/95. GPS reading: 71° 32. 958′ North, 22° 55.188' West, elevation 2200 feet.
12/G95:	?Eggshell. Upper limestone above Stairmaster Quarry. WWA collected 7/31/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.
13/G95:	Nodule with reptilian bone. Upper limestone above Stairmaster Quarry. WWA collected 7/31/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.
14/G95:	Partial jaw, many teeth lacking crowns, probably amphibian. Goldberg's Tongue: WRD locality. FAJJr collected 8/2/95. GPS reading: 71° 31.793′ North, 22° 50.668' West, elevation 1900 feet.
15/G95:	Morganucodontid molariform tooth. Goldberg's Tongue: WRD locality. WRD collected 8/2/95. GPS reading: 71° 31.793′ North, 22° 50.668' West, elevation 1900 feet.
16/G95:	?Maxilla and ?lissamphibian-like femur. Goldberg's Tongue: WRD locality. WRD collected 8/2/95. GPS reading: 71° 31.793′ North, 22° 50.668' West, elevation 1900 feet.
17/G95:	Sample blocks for acid processing in laboratory. Goldberg's Tongue: WRD locality, a thin limestone lens of restricted areal extent yielding specimens 14/G95, 15/G95 and 16/G95; these additional samples include a humerus and vertebrae. Collected by party 8/2 - 8/3/95. GPS reading: 71° 31.793′ North, 22° 50.668' West, elevation 1900 feet.



Field List: Greenland Expedition 1995 - continued

18/G95: Samples of upper limestones above Stairmaster Quarry for acid processing in laboratory. Collected by SMG, WWA, NHS during latter stages of Stairmaster satellite operation. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.

19/G95: ?Mammalian molar. Upper limestone above Stairmaster Quarry. SMG collected 8/1/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.

20/G95: Maxilla, unknown taxonomic affinity (labelled "int."). Upper limestone above Stairmaster Quarry. NHS collected 8/1/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.

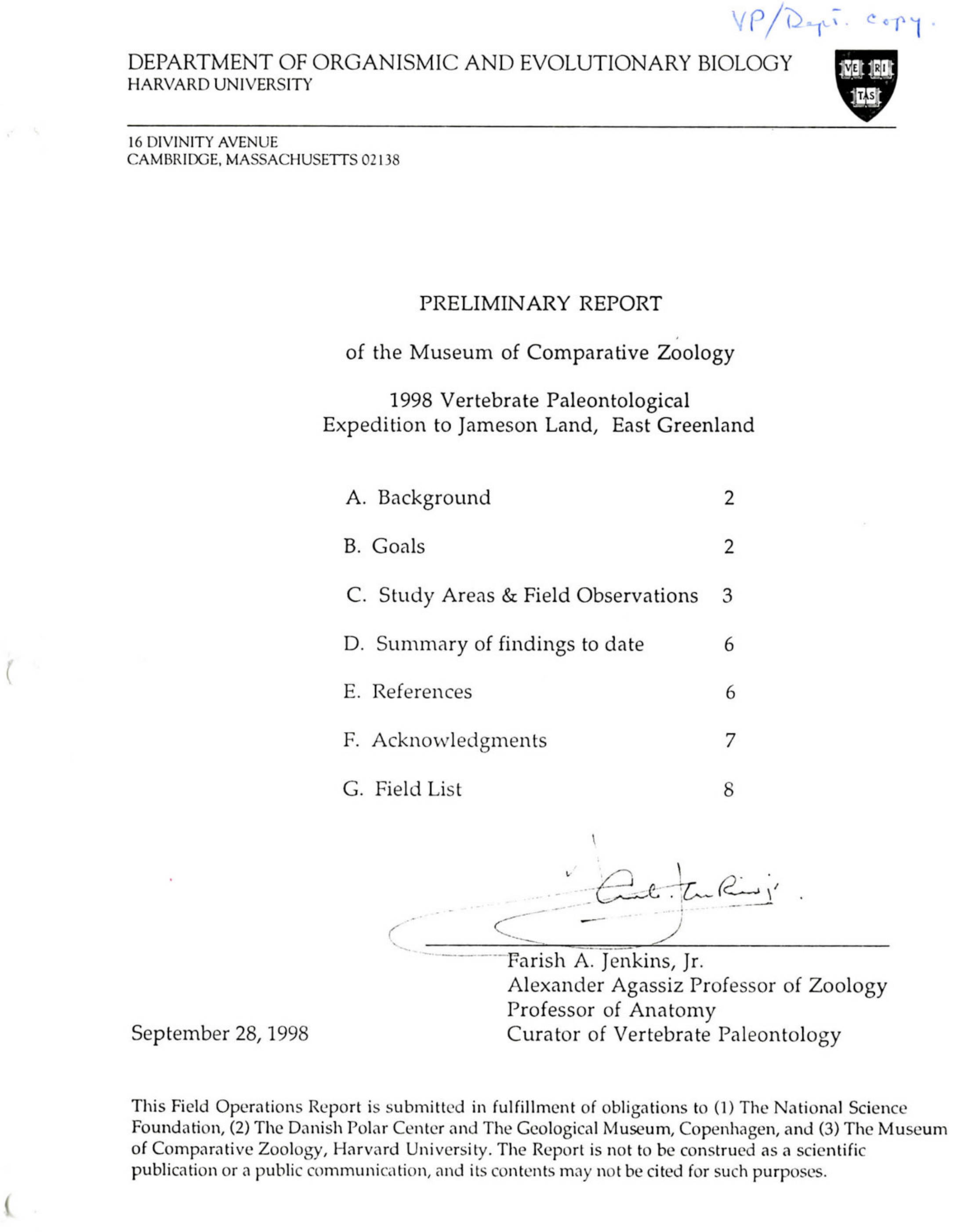
21/G95: Associated ?reptilian postcranial bones. Upper limestone above Stairmaster Quarry. WWA collected 8/1/95. GPS reading: 71° 32.958′ North, 22° 55.188' West, elevation 2200 feet.

22/G95: Large tooth with flange (ca. 4 cm). Stairmaster Quarry. MDS collected *circa* 7/15/95. GPS reading: 71° 32.611′ North, 22° 55. 307′West, elevation 1900 feet.

23/G95: Yellow and purple limestone samples from shoulder south of Camp XI accessed by musk oxen path. FAJJr collected 8/6/95.
GPS reading: 71° 31.158′ North, 22° 56.908′ West, elevation 1200 feet.

A10 – Field report 1998 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 1998 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



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DEPARTMENT OF ORGANISMIC AND EVOLUTIONARY BIOLOGY
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PRELIMINARY REPORT

of the Museum of Comparative Zoology

1998 Vertebrate Paleontological
Expedition to Jameson Land, East Greenland

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September 28, 1998

This Field Operations Report is submitted in fulfillment of obligations to (1) The National Science Foundation, (2) The Danish Polar Center and The Geological Museum, Copenhagen, and (3) The Museum of Comparative Zoology, Harvard University. The Report is not to be construed as a scientific publication or a public communication, and its contents may not be cited for such purposes.

A. BACKGROUND

The 1998 Vertebrate Paleontological Expedition to East Greenland was conducted with the financial assistance of a research grant from the U.S. National Science Foundation (Grant No. 97-14975), and with the permission of the Danish Commission for Scientific Research in Greenland. This expedition, the sixth field season spent in Jameson Land (see Reports previously submitted for 1988, 1989, 1991, 1992 and 1995), operated for a period of thirty-three days from 3 July through 5 August, 1998. Field work this season was adversely affected by more than the usual few bouts of inclement weather; approximately 11.5 days (ca. 35% of time) were lost to inoperable conditions. The expedition was led by Professor Farish A. Jenkins, Jr., and staffed by: Mssrs. William W. Amaral, Leon Claessens, Charles R. Schaff, Michael D. Shapiro, and Tomasz Owerkowicz (Harvard University); Associate Professor Neil H. Shubin and Mr. Marcus C. Davis (University of Pennsylvania); Assistant Professor Stephen M. Gatesy and Mr. Kevin M. Middleton (Brown University).

B. GOALS

1) Mammals and other microvertebrates.

The project was designed to pursue opportunities to advance our knowledge of the morphology, functional anatomy and phylogeny of early mammals that developed as the result of the recent discovery of associated remains of a haramiyid in the upper Fleming Fjord Formation of East Greenland (between 71-72°N). Long known from European Late Triassic deposits only from isolated teeth, haramiyids (among the earliest known fossil evidence of mammals) have been interpreted as related to multituberculates, but their relationships remained nonetheless enigmatic because of uncertainties of tooth orientation and identity; even their mammalian status had been questioned. The new Greenlandic haramiyid exhibits no close relationship to multituberculates on the basis of its highly specialized dentition, but retains features of the jaw and postdentary apparatus that would place the family in a basal position among mammals. The discovery not only reveals greater diversity among early mammals than previously known, but also demonstrates how readily the current conceptual framework of early mammalian evolution, based on a few, quite incompletely known taxa, made be reordered by new evidence.

Field program in the Fleming Fjord Formation in 1998 concentrated on stratigraphic levels and lithologies that offered the best prospects for recovering additional mammalian and microvertebrate materials. The red mudstone, red mudstone-gray sandstone, and light-colored carbonate facies associations of the Tait Bjerg Beds, which formed under cyclic, continental conditions and represent lacustrine, fluviatile, overbank and subaerial settings, are widespread in both geographic extent and exposure in the Jameson Land Basin. Preliminary surveys of these beds in previous years (which yielded, in addition to haramiyid material, an associated skull and jaws of a small ?crocodilomorph) indicated several lithological regimes that concentrated microvertebrates with more complete skeletal association than is characteristic of other Upper Triassic localities elsewhere (where isolated teeth and fragments predominate).

Fossils from Late Triassic times are critical to evaluating current hypotheses of relationship among Mesozoic mammals as well as providing definitive evidence with which to interpret the major transformations in the masticatory, auditory, neurocranial, appendicular and postcranial axial systems. Inasmuch as so few taxa of 'Rhaeto-Liassic' mammals are known in any detail other than dental structure, the realistic prospect of recovering additional associated mammalian skeletal material from the Fleming Fjord Formation offered excellent potential to increase significantly our knowledge of the early history of Mammalia.

2) Paleoichnology. A second objective of the expedition was to continue studies of the extensive exposures of dinosaur tracks located on the eastern shoulder of Wood Bjerg, informally known as the "Raceway" locality. This work, undertaken by Professor Stephen M. Gatesy, is part of a larger, ongoing study of locomotion and tracking by living birds in Dr. Gatesy's laboratory at Brown University.

3) Palynology. A third objective was to collect samples suitable for palynological analysis. Previous study of palynofloras from the Rhaetian and Hettangian Kap Stewart Formation, which overlies the Fleming Fjord Formation, have determined that these assemblages differ from latest Triassic assemblages elsewhere in Europe and North America (Pedersen and Lund, 1980). The Greenland assemblages contain more species of spores and lack abundant gymnosperm pollen of the genus *Corollina*, the dominant taxa of many Late Triassic and Early Jurassic palynofloras. Given the similarity of Fleming Fjord vertebrate fossils to Norian faunas of Europe (Jenkins et al., 1994), the palynofloral composition of this formation is of particular interest for biostratigraphic correlation and temporal assessment. Dates derived from pollen and spore assemblages of the Gipsdalen and Fleming Fjord Formations are expected to rule out one of two possible correlations with the Newark Basin magnetic reversal time scale (Kent and Clemmensen, 1996). Palynological analysis also has the potential to contribute climatic and environmental evidence that will test previous interpretations based on sedimentology (Clemmensen, Kent and Jenkins, 1998).

C. AREAS OF STUDY AND FIELD OBSERVATIONS

Paleontological reconnaissance, excavation and collecting were undertaken from four base camps and one satellite camp from which local exposures were surveyed; all of these areas lie within the southern half of the Triassic rift valley basin as interpreted by L. B. Clemmensen.

Camp XII (3 July - 7 July): 71° 33.544' North, 23° 3.884' West, elevation approximately 1,000 feet. This area represented a new prospect, and it was hoped that the lithologies and preservational regimes would be comparable to that of the *Haramiyavia* locality. The base camp was situated on the east face of the ridge separating Pingel Dal and Enhjørningens Dal. Exposures of the Ørsted Dal Member and Tait Bjerg Beds of the Fleming Fjord Formation north of the base camp were extensively examined by all members of the expedition during this four day period. Exposures of the uppermost strata of the Fleming Fjord Formation, comparable to those of the *Haramiyavia* locality at Ærenprisdal, were found to be present on the cliff face of the east side of the ridge; the same beds on the top and west face of the ridge were largely reworked by erosion and slumping, and were generally unsuitable for paleontological prospecting. Although some fish remains and tetrapod (primarily amphibian) cranial and postcranial bones, all disarticulated and/or incomplete, were discovered in limestone lenses at several localities (notably 71° 34.708' N, 23° 4.976'W; and 71° 34.775'N, 23° 5.128'W), the sediments themselves had been disrupted and transported in the process of weathering. Intensive inspection of the sediments in this area demonstrated little potential for vertebrate fossils of scientific value, and a camp displacement to the next area was arranged earlier than had been anticipated in the Field Operations Plan.

Camp II (7 July - 16 July): 71° 15.86'N, 22° 32.37'W, elevation approximately 1,000 feet. The western side of the Paselv valley at the head of Carlsberg Fjord, bounded to the north by Lepidopteriselv, presents an extensive, moderately sloping exposure of the Ørsted Dal Member of the Fleming Fjord Formation, and a limited exposure of the Tait Bjerg Beds that represent the uppermost part of the formation. Although this area had been previously surveyed by Harvard parties in 1989 and 1991, two possibilities invited renewed effort: a quarriable site (71° 16.031'N, 22° 31.805'W) discovered in 1991 but only briefly worked, and a closer examination of the Tait Bjerg Beds. However, with the exception of an assemblage of *Gerrothorax* skeletal elements (Field number G98/5), extensive quarrying at this site by seven expeditionary members revealed only disarticulated, partial amphibian bones. Likewise, the Tait Bjerg Beds in this area, which in general are highly weathered, or covered by skree from the overlying Kap Stewart Formation, proved unproductive. However, theropod trackways were discovered in a sandstone lens (upper Ørsted Dal Beds) 100m south of the base camp, and two of these were collected (Field numbers G98/3 and G98/4) for use in the ongoing trackway studies being conducted by S. M. Gatesy *et aliter*. A partial skull of a very small *Gerrothorax* (Field number G98/1) was collected from the upper Ørsted Dal Beds at 71° 15' 34.9"N, 22° 33' 01.5"W. Additional cranial material of a juvenile prosauropod specimen (Field number G98/2; 71° 16.485'N, 22° 32.263'W), first encountered during the 1989 field season, were recovered by dry screening; the specimen appears to be quite incomplete, the enclosing sediments having been disturbed by a volcanic sill. Two large prosauropod specimens, represented by substantial bone fragments weathering out of mudstones of the uppermost Ørsted Dal Beds, were located, respectively, at 71° 16.485'N, 22° 32.263'W and 71° 16.365'N, 22° 32.318'W. The specimens were not collected because of the time commitment required, and in any case these specimens did not fall within the purview of the present project; their location is here noted for future reference.

Raceway satellite camp (16 July - 20 July): 71° 24.88'N, 22° 33.17'W, elevation 1,760 feet. The "Raceway" locality, where an extensive array of dinosaurian footprints have been exposed by aeolian scouring of the upper Ørsted Dal Beds, was discovered in 1989 and subsequently studied in detail by Professor S. M. Gatesy in 1991-92 and 1995. A manuscript detailing the significance of these trackways is near completion by Gatesy, K. M. Middleton, N. H. Shubin and F. A. Jenkins, Jr. The goal of this year's field work was to re-examine the entire suite of prints to verify the consistency of interpretations made previously, and to collect additional representative specimens for further dissection and analyses. These goals were met by Gatesy, Middleton, Shubin and Jenkins during the four day period, despite some unfavorable weather conditions. Eight tracks were collected (which were transported to Constable Pynt by Air Alpha helicopter on 25 July). The party of four displaced on foot to Camp XIII on 20 July.

Camp XIII (16 July - 25 July): 71° 28.446'N, 22° 43.723'W, elevation approximately 1,000 feet. Exposures surveyed from this base camp included the extensive section of the Fleming Fjord Formation on Tait Bjerg (to the east) as well as exposures along the south side of Ærenprisdal and the intersection of the head of this valley with that of Permdal. The base camp was selected because it was central to this extensive area in which there is considerable exposure of Tait Bjerg Beds equivalent to those of the *Haramiyavia* locality. The results were disappointing, however. Although several fish jaws and associated materials were collected (Field numbers G98/6, 7, 8 and 9), no scientifically useful tetrapod fossils were found. Additionally, field work here was hampered by sustained bouts of inclement weather. Displacement to Ærenprisdal Base Camp XI was made two days earlier than anticipated in the Field Operations Plan because that area seemed now to afford more promising collecting opportunities.

Camp XI (25 July - 5 August): 71° 32.106'N, 22° 58.559'W. The base camp, established on the eastern side of Pingel Dal at the confluence of the Ærenprisdal drainage with another stream draining the elevated terrain south of Ærenprisdal, provided access to four areas, all of which offered potentially fossiliferous exposures of the uppermost Fleming Fjord Formation. (1) The "Stairmaster" locality (71° 32.611'N, 22° 55.307'W), which yielded *Haramiyavia* and other microvertebrates in 1995, required an approximately 2,000 foot ascent from base camp. This locality was extensively and intensively surveyed by almost all expeditionary members, and bone-rich matrix samples were collected for acid processing and laboratory examination. (2) The highland area directly ESE of Camp XI also received intensive prospecting. Several richly fossiliferous layers were examined in detail, and matrix samples from three of them collected for laboratory processing ("Divide North": 71° 30.732'N, 22° 46.001'W; "Divide Streambed MDS locality": 71° 30.565'N, 22° 46.116'W; "CRS Thunderdome locality": 71° 31.397'N, 22° 48.245'W). A partial skull, probably archosaurian and possibly theropodan, was collected from the "Thunderdome" locality (11/98G); additionally, a very large skull (approximately 1m across the occiput, 83 cm occipito-rostral length) of a (?cyclotosaur) amphibian was identified, but most of the skull had weathered/broken away and the specimen was deemed not worth attempting to salvage. Several efforts were made to relocate the 1991 mammal site located near the "Divide North" locality but residual snow cover precluded a definitive search. 3) The summit of Kassen, an 890m ridge NW of base camp, presents exposures of the uppermost Fleming Fjord Formation. These were surveyed by five members of the expedition on 27 July who reported a few fragmentary fish remains but no tetrapod fossils of interest. 4) Exposures of the upper Ørsted Dal Beds on the highlands 500m directly south of Ærenprisdal base camp. These were surveyed by two members of the expedition on 29 July; the uppermost part of the Fleming Fjord Formation were found to be largely eroded away in this area (save for some skree blocks from Tait Bjerg Beds mixed with a Kap Stewart skree slide).

D. SUMMARY OF FINDINGS TO DATE FROM THE 1998 EXPEDITION

Despite the impact of adverse weather on working conditions, the expedition was able to survey all of the areas scheduled in the Field Operations Plan. The goals of the "Raceway" dinosaur track project were fully met. A substantial collection of richly concentrated bone-bearing matrix from several localities was acquired for laboratory processing and study. These same samples will serve also for palynological analysis. Despite the extensive efforts by expeditionary personnel and the successful coverage of the prime target regions, no new microvertebrate taxa were identified in the field, but it is yet hoped that these small and important fossils will emerge as laboratory work proceeds.

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F. ACKNOWLEDGMENTS

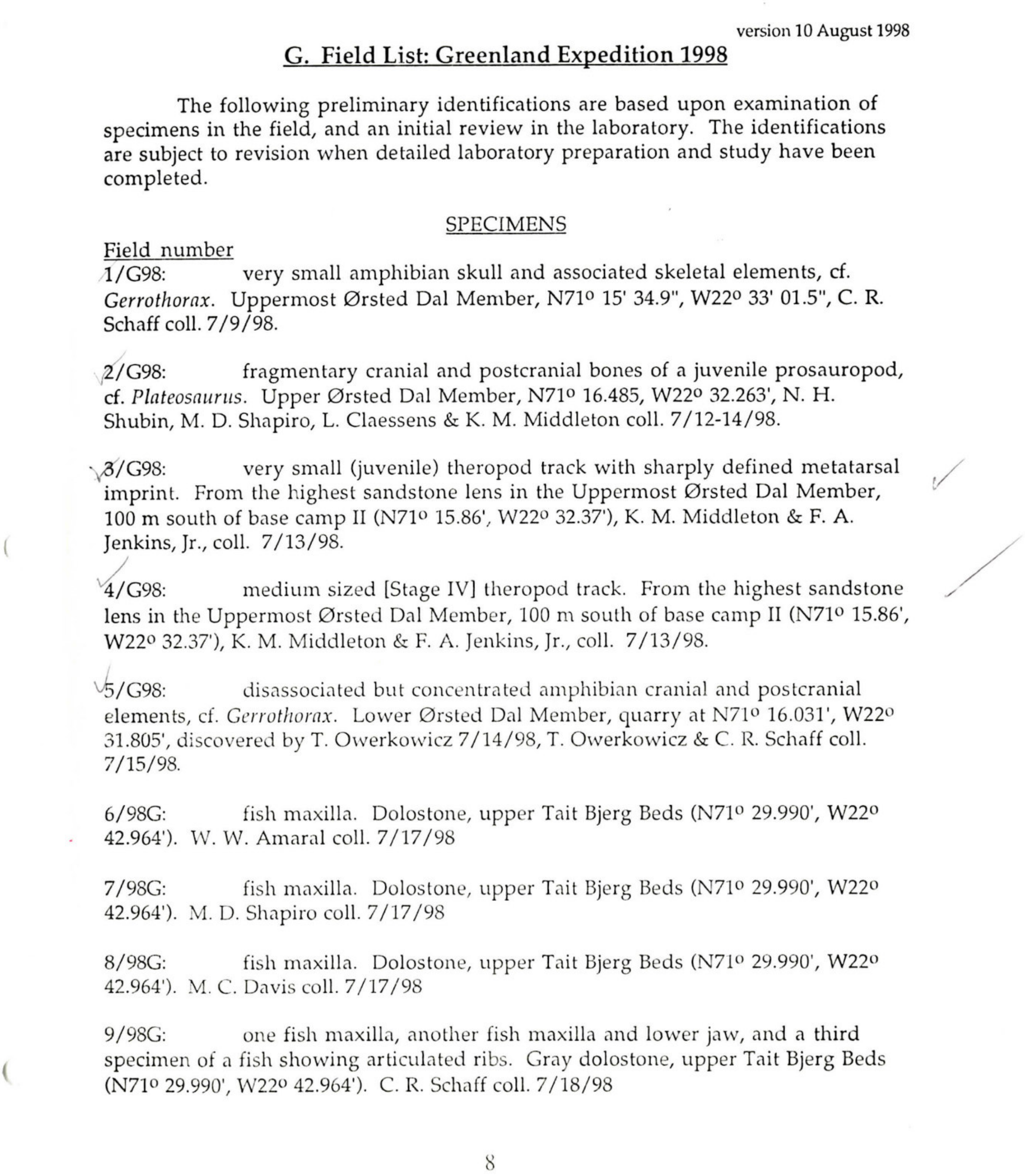
We are grateful to the National Science Foundation (Division of Polar Programs), and especially to Dr. Douglas Siegel-Causey for his interest in and support of this project. We thank the Commission for Scientific Research in Greenland for permission to undertake field work in Jameson Land.

Once again we salute the extraordinary efforts of Mr. T. I. Hauge Andersson of the Dansk Polar Center for his highly efficient management of logistical operations before the expedition, and acknowledge with warmest thanks Mr. Karsten Nielsen for his faithful radio contacts and adept coordination of our changing plans.

We are especially indebted to the skill and good services of Captain Per Jennings of Air Alfa for helicopter-shuttling of personnel and supplies between camps and field sites.

We extend thanks to the Icelandic and United States personnel at the U. S. Naval Air Station, Keflavik, Iceland, for their helpfulness in transferring personnel and cargo to and from Greenland, and particularly wish to acknowledge Lieutenant Robert W. Yarosz, USN, for his assistance.

Finally, we extend our thanks the flight officers of Flugfelag Islands, a flying company that always can be counted on, and are grateful to Mr. Fridrik Adólfsson (IcelandAir, Greenlandic operations) for logistical arrangements.



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G. Field List: Greenland Expedition 1998

The following preliminary identifications are based upon examination of specimens in the field, and an initial review in the laboratory. The identifications are subject to revision when detailed laboratory preparation and study have been completed.

SPECIMENS

Field number

1/G98: very small amphibian skull and associated skeletal elements, cf. *Gerrothorax*. Uppermost Ørsted Dal Member, N71° 15' 34.9", W22° 33' 01.5", C. R. Schaff coll. 7/9/98.

2/G98: fragmentary cranial and postcranial bones of a juvenile prosauropod, cf. *Plateosaurus*. Upper Ørsted Dal Member, N71° 16.485, W22° 32.263', N. H. Shubin, M. D. Shapiro, L. Claessens & K. M. Middleton coll. 7/12-14/98.

3/G98: very small (juvenile) theropod track with sharply defined metatarsal imprint. From the highest sandstone lens in the Uppermost Ørsted Dal Member, 100 m south of base camp II (N71° 15.86', W22° 32.37'), K. M. Middleton & F. A. Jenkins, Jr., coll. 7/13/98.

4/G98: medium sized [Stage IV] theropod track. From the highest sandstone lens in the Uppermost Ørsted Dal Member, 100 m south of base camp II (N71° 15.86', W22° 32.37'), K. M. Middleton & F. A. Jenkins, Jr., coll. 7/13/98.

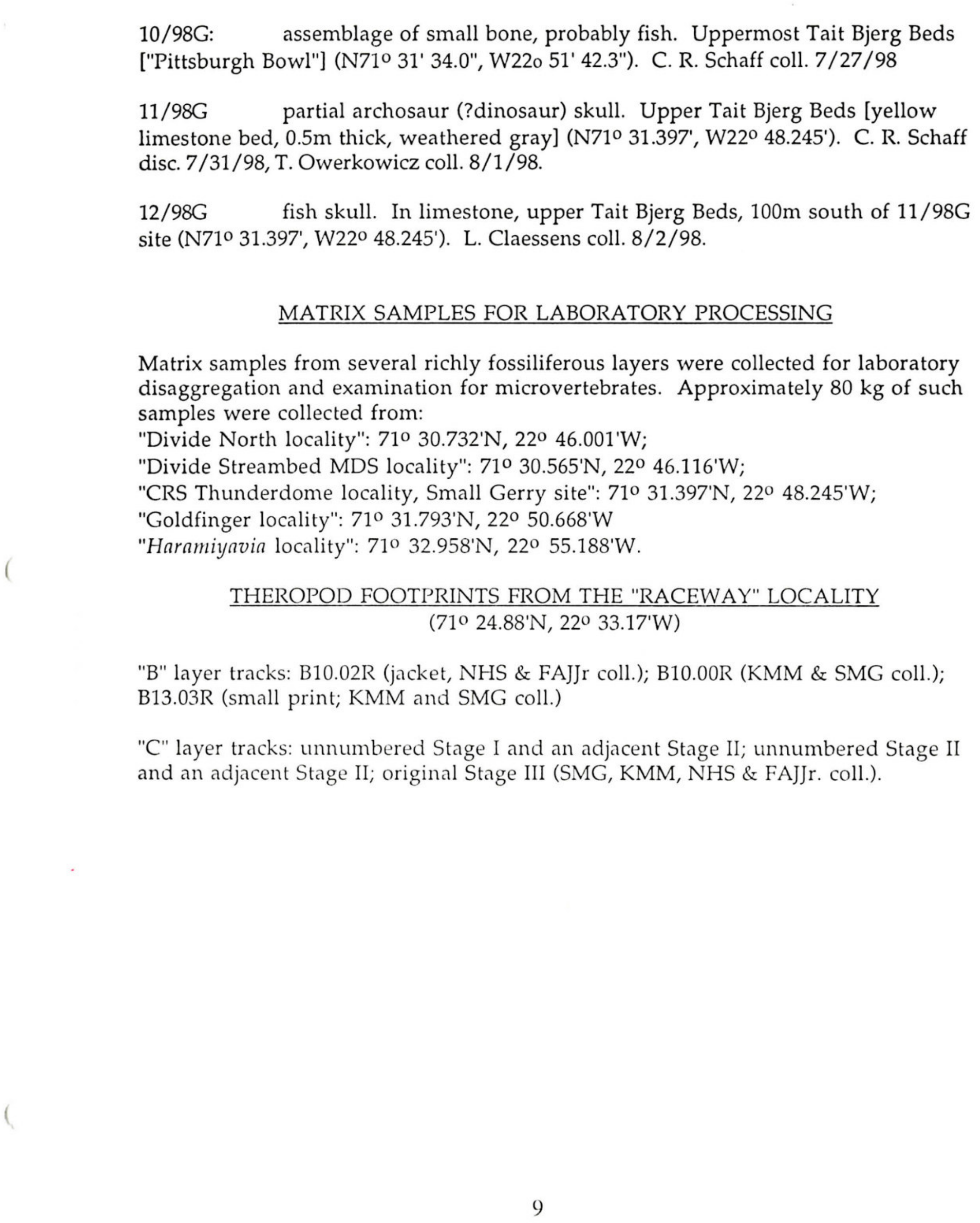
5/G98: disassociated but concentrated amphibian cranial and postcranial elements, cf. *Gerrothorax*. Lower Ørsted Dal Member, quarry at N71° 16.031', W22° 31.805', discovered by T. Owerkowicz 7/14/98, T. Owerkowicz & C. R. Schaff coll. 7/15/98.

6/98G: fish maxilla. Dolostone, upper Tait Bjerg Beds (N71° 29.990', W22° 42.964'). W. W. Amaral coll. 7/17/98

7/98G: fish maxilla. Dolostone, upper Tait Bjerg Beds (N71° 29.990', W22° 42.964'). M. D. Shapiro coll. 7/17/98

8/98G: fish maxilla. Dolostone, upper Tait Bjerg Beds (N71° 29.990', W22° 42.964'). M. C. Davis coll. 7/17/98

9/98G: one fish maxilla, another fish maxilla and lower jaw, and a third specimen of a fish showing articulated ribs. Gray dolostone, upper Tait Bjerg Beds (N71° 29.990', W22° 42.964'). C. R. Schaff coll. 7/18/98



10/98G: assemblage of small bone, probably fish. Uppermost Tait Bjerg Beds ["Pittsburgh Bowl"] (N71° 31' 34.0", W22o 51' 42.3"). C. R. Schaff coll. 7/27/98

11/98G partial archosaur (?dinosaur) skull. Upper Tait Bjerg Beds [yellow limestone bed, 0.5m thick, weathered gray] (N71° 31.397', W22° 48.245'). C. R. Schaff disc. 7/31/98, T. Owerkowicz coll. 8/1/98.

12/98G fish skull. In limestone, upper Tait Bjerg Beds, 100m south of 11/98G site (N71° 31.397', W22° 48.245'). L. Claessens coll. 8/2/98.

MATRIX SAMPLES FOR LABORATORY PROCESSING

Matrix samples from several richly fossiliferous layers were collected for laboratory disaggregation and examination for microvertebrates. Approximately 80 kg of such samples were collected from:
"Divide North locality": 71° 30.732'N, 22° 46.001'W;
"Divide Streambed MDS locality": 71° 30.565'N, 22° 46.116'W;
"CRS Thunderdome locality, Small Gerry site": 71° 31.397'N, 22° 48.245'W;
"Goldfinger locality": 71° 31.793'N, 22° 50.668'W
"*Haramiyavia* locality": 71° 32.958'N, 22° 55.188'W.

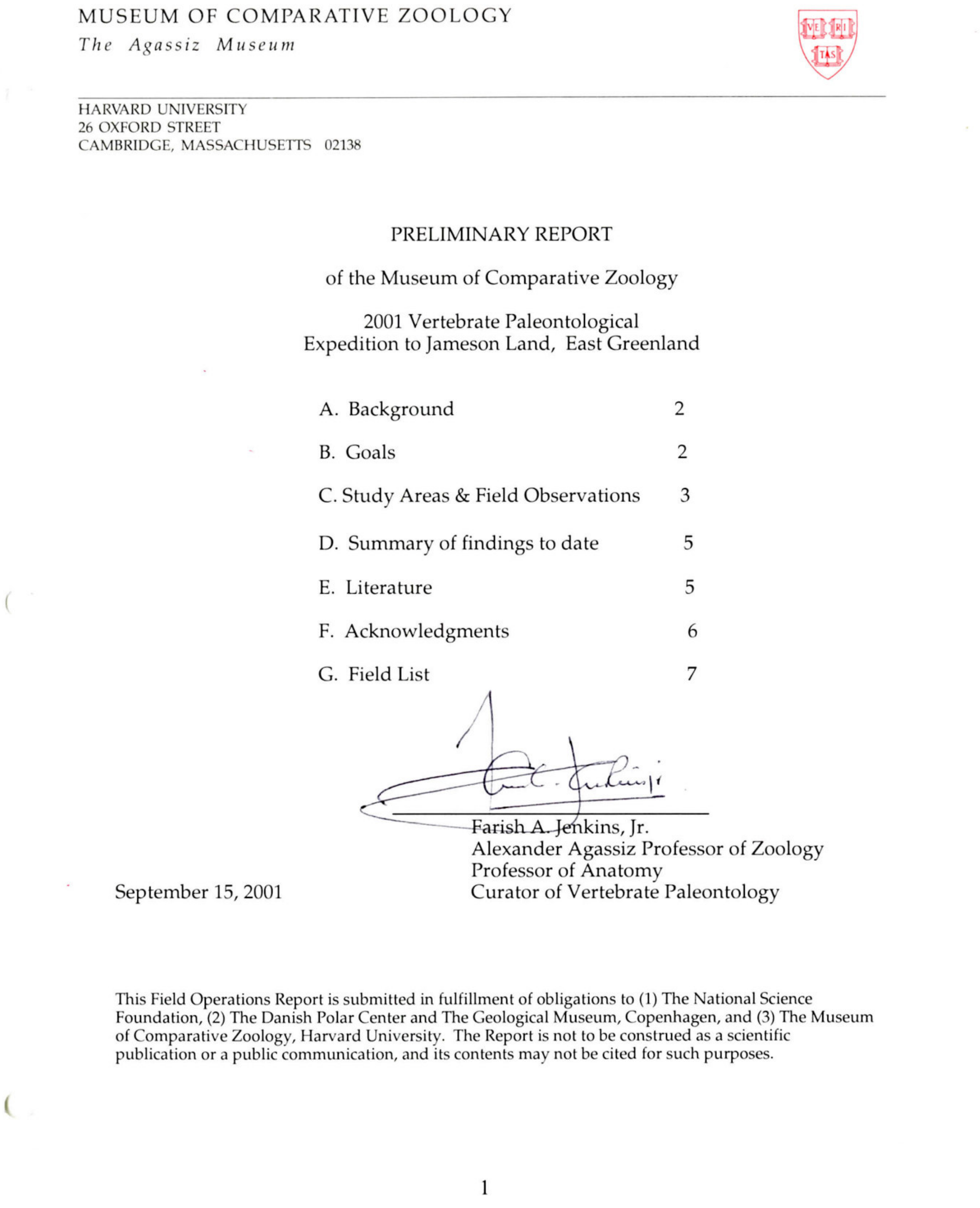
THEROPOD FOOTPRINTS FROM THE "RACEWAY" LOCALITY
(71° 24.88'N, 22° 33.17'W)

"B" layer tracks: B10.02R (jacket, NHS & FAJJr coll.); B10.00R (KMM & SMG coll.); B13.03R (small print; KMM and SMG coll.)

"C" layer tracks: unnumbered Stage I and an adjacent Stage II; unnumbered Stage II and an adjacent Stage II; original Stage III (SMG, KMM, NHS & FAJJr. coll.).

A11 – Field report 2001 expedition

Preliminary report of the Museum of Comparative Zoology (Harvard University) – 2001 Vertebrate Paleontological Expedition to Jameson Land, Eastern Greenland



MUSEUM OF COMPARATIVE ZOOLOGY
The Agassiz Museum

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PRELIMINARY REPORT

of the Museum of Comparative Zoology

2001 Vertebrate Paleontological
Expedition to Jameson Land, East Greenland

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Farish A. Jenkins, Jr.
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September 15, 2001 Curator of Vertebrate Paleontology

This Field Operations Report is submitted in fulfillment of obligations to (1) The National Science Foundation, (2) The Danish Polar Center and The Geological Museum, Copenhagen, and (3) The Museum of Comparative Zoology, Harvard University. The Report is not to be construed as a scientific publication or a public communication, and its contents may not be cited for such purposes.

A. BACKGROUND

The 2001 Vertebrate Paleontological Expedition to East Greenland was conducted with the financial assistance of a research grant from the U.S. National Science Foundation (OPP 97-14975), with the permission of the Danish Commission for Scientific Research in Greenland, and with the support of the Danish Polar Center. This expedition, the seventh field season spent in Jameson Land (see Reports previously submitted for 1988, 1989, 1991, 1992, 1995 and 1998), operated for a period of thirty-three days from 28 June through 30 July, 2001. Field work this year was not seriously impacted, as had been the case in some previous years, by inclement weather; only during the period 16 – 19 July did poor weather curtail operations. The expedition was staffed by Professor Farish A. Jenkins, Jr., (Harvard University), Professor Stephen M. Gatesy (Brown University), Mr. William W. Amaral (Manager of the Preparation Laboratory, Department of Vertebrate Paleontology, Museum of Comparative Zoology, Harvard University) and Mr. Kevin M. Middleton (Ecology and Evolutionary Biology Graduate Program, Brown University).

B. GOALS

1) Mammals and other microvertebrates. The project was designed to pursue opportunities to advance our knowledge of the morphology, functional anatomy and phylogeny of late Triassic mammals, reptiles and amphibians. The discovery of associated remains of a haramiyid in the upper Fleming Fjord Formation at Ærenprisdal in 1995 (Jenkins, Gatesy, Shubin and Amaral, 1997; see reference list appended) represented an important advance in our understanding of early mammals. Haramiyids posed a particularly difficult problem for paleontologists because their teeth were unlike those of any other mammal, and thus even their mammalian affinities had been open to question. The Greenlandic discovery settled these questions: haramiyids are definitely mammals but represent a substantially divergent branch in early mammalian evolution. From the same locality was obtained the lower jaw of a small cynodont (Shapiro and Jenkins, 2001) that exhibited a curious and heretofore unknown mixture of cynodont and mammalian features. Although this new taxon clearly possesses double-rooted postcanine teeth, a feature previously believed to be restricted entirely to mammals (with the exception of tritylodontids), the dentition evidences no wear facets that would be indicative of mammalian occlusion. Furthermore, the taxon possesses an alternative pattern of tooth replacement that is distinctively cynodont-like, and non-mammalian. Previously, paleontologists widely believed that diphyodonty (two sets of dentitions– a juvenile and an adult set of teeth), double rootedness, and tooth-to-tooth occlusion that produces wear facets represented an interdependent complex of characters that evolved among early mammals. It is now known from the Ærenprisdal cynodont that these characters are independent, and one of them, at least, evolved among cynodonts, rather than mammals.

The novelty and importance of these microvertebrate specimens prompted us to conduct a wide ranging survey of the uppermost dolostones (Tait Bjerg Beds) of the Fleming Fjord Formation in the hopes of discovering a locality comparably fossiliferous to that at Ærenprisdal.

2) Paleoichnology. Our second objective was to continue studies of theropod

dinosaur trackways that are preserved within many layers of the Ørsted Dal and Tait Bjerg Beds. Some of these trackways preserve three-dimensional records of theropod foot movement (see Gatesy, Middleton, Jenkins, and Shubin, 1999) as well as provide clear skin impressions that also serve as indicators of foot movement (Gatesy, 2001). Although the original field operations plan called for us to survey Lamprenens Dal for dinosaur tracks previously reported by mineral surveyors in 1991, we bypassed this area once we discovered, through visual reconnaissance from Gurreholm Bjerge, that overlying intrusive sills largely covered the exposures of the Fleming Fjord Formation with skree. As indicated in the original survey report, the tracks were in "sandstone blocks," and this is consistent with our visual inspection that revealed little, if any, possibility of finding extensive exposures of trackway bearing sediments in place. Trackway studies were therefore conducted at other localities (see below).

C. AREAS OF STUDY AND FIELD OBSERVATIONS

Paleontological reconnaissance and collecting were undertaken from four base camps and one satellite camp that provided access to local exposures; all of these areas lie within the southern half of the Triassic rift valley basin as interpreted by L. B. Clemmenson (1980 a,b).

Camp XIV (28 June – 1 July). Gurreholm Berg, 71° 43.920′ North, 23° 49.197′ West, altitude approximately 3200 feet. This area represented a new prospect, and it was hoped that the lithologies and preservational regimes would be comparable to that of the Ærenprisdal locality. Unfortunately, an extensive residual snow cover (60-80%) at this elevation precluded access to many areas. Although extensive areas of the upper Fleming Fjord Formation are indicated on the GGU map, many of these were found to be masked by solifluction or skree, and thus unsuitable for paleontological prospecting. In face of such contrary indicators, the decision was quickly made to move to our next objective in the Field Operations Plan.

Camp XV (2 – 5 July). Southwest flank of Schröter Bjerge, North 71° 41.243′, 23° 11.386′ West, elevation 1245 feet. Our original intent, as outlined in the Field Operations Plan, was to examine exposures mapped on Didrik Pining Berg in the vicinity of Allday Dal and Qoroq, but it became all too evident to FAJJr and WWA during the inbound helicopter flight that exposures of the Upper Fleming Fjord Formation were very limited by the same factors that adversely impacted our operation on Gurreholm Berg. An *ad hoc* decision was therefore made to set our camp in the vicinity of the type section of the Malmros Klint, thus providing us with an opportunity to seek exposures of the top of the section along the southeastern facing cliffs of Schröter Bjerge. In three successive days we were able to conduct an extensive reconnaissance of suitable exposures of the upper part of the Fleming Fjord Formation, but without material success in terms of fossils or trackways. Binocular survey across Fleming Fjord, however, revealed the next likely prospect in a mountain area between Lille Cirkusbjerg and Dansen circa 71° 38′ North, 22° 57′ West. Accordingly, we elected to shift base camp again.

Camp XVI (6 July – 9 July): North 71° 37.560′, West 22° 55.769′, elevation 2625 feet, on the western flank of Lille Cirkusbjerg. This camp, like that on Gurreholm Berg, placed us in a relatively exposed position, with almost no running water, and the attendant risk that, should it rain, the ground surface of the basal sediments of the Kap Stewart Formation

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would be quickly transformed into a morass of mud. We thus had heightened incentive to accomplish our work here quickly and efficiently. Exposures of the Upper Fleming Fjord Formation here were narrow in extent (100 meters or less), but extended east-west for some three kilometers. Although the exposures were excellent (free of slumpage and debris), there was scant trace of fossils and only a few poorly preserved dinosaur tracks. The area was thoroughly surveyed during this period.

Camp VI (10 – 30 July). Southwestern side of Tait Berg, North 71° 28.318′, West 22° 40.665′, elevation 880 feet. The decision to move to this previously used camp was prompted by our knowledge that it was central to a very large area of Fleming Fjord exposures, and in particular offered extensive opportunities to examine the uppermost beds near or at the contact with the overlying Kap Stewart Formation. Likewise it was realized that in the course of the 1998 and present field season, we had exhausted all other known possibilities for examining stratigraphic levels comparable to that at Ærenprisdal, which had yielded important fossils. We therefore remained at this camp for the remainder of the field season which, with the exception of the period 16-19 July, was dominated by excellent weather conditions that permitted extensive and detailed examinations of Tait Berg to the northeast, and localities as far west as North 71° 30.732′, 22° 46.001′ West.

On 20 July we employed the helicopter for the purpose of 1) conveying SMG and KMM to the "Raceway" locality on Woodberg (71° 24.88′ North, 22° 33.17′ West, elevation 1760 feet) where they were to pursue "prosauropod" trackways that had not received as extensive attention in the past as had the theropod tracks; 2) to survey and examine on foot exposures on Buch Berg that were either inaccessible from Camp VI or could not be used as base camp sites because of the lack of water. During this reconnaissance the helicopter conveyed FAJJr, WWA and KMM to the west shoulder of Buch Berg at North 71° 31.31′, West 22° 42.41′. 200 meters west of the landing site a fossiliferous lens was identified and a sample of matrix collected for laboratory examination.

SMG and KMM worked at the "Raceway" locality intensively for three days, returning to Camp VI on 23 July on foot, crossing Passagen in three hours. The residual camp supplies and scientific samples from this satellite camp were picked up by helicopter on our departure 30 July. SMG and KMM continued their studies of dinosaur footprints exposed on the extensive exposures of the Ørsted Dal Beds that occur on the southwest flank of Tait Berg.

Despite concerted efforts, the upper part of the Fleming Fjord Formation (stratigraphically equivalent to the fossiliferous layer at Ærensprisdal) proved largely barren of significant vertebrate fossils. Several hand samples were collected for laboratory breakdown and examination, notably from North 71° 28.533′, West 22° 41.839′; North 71° 28.13′, West 22° 41.284′; and North 71° 28.669′, West 22° 39.249′. The most promising locality was discovered by WWA on the 29 July – not at the top of the section, but low in the Ørsted Dal Beds (North 71° 28.421′, West 22° 38.839′, elevation 1400 feet). Several postcranial fragments in the bone rich matrix appeared to be suggestive of mammalian remains, with evidence that this highly localized sedimentary regime was sorting for small long bones. As much of this matrix as could be found was collected for detailed preparation in the laboratory.

D. SUMMARY OF FINDINGS TO DATE FROM THE 2001 EXPEDITION

The expedition completed its objective of surveying all of the areas known to offer exposures of the uppermost Fleming Fjord Formation. The trackway studies by SMG and KMM were particularly successful in identifying, recording, or collecting trackways of good quality (some with skin impressions) that, with further study, may extend our understanding of dinosaurian locomotion. Although our collections of bone-bearing matrix are relatively limited, we remain hopeful that these may contain microvertebrate materials that are as yet unknown to science, and that will repay our exertions across the demanding landscape of East Greenland.

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version 14 September 2001

G. FIELD LIST: GREENLAND EXPEDITION 2001

MATRIX SAMPLES FOR LABORATORY PROCESSING

Matrix samples (totally approximately 75 kg.) from several fossiliferous layers were collected for laboratory disaggregation and examination for microvertebrates.
Tait Bjerg: 71° 28.669′N, , 22° 39.249′W; WWA coll. 7/25.01,
Field no. G01/1, partial amphibian jaw in bone layer matrix.
Tait Bjerg: 71° 28.553′N, , 22° 41.839′W; WWA coll. 7/14/01,
Field no. G01/sample 1.
Tait Bjerg west: 71° 28.136′N, 22° 41.284′W; FAJJr coll. 7/21/01,
Field no. G01/sample 2.
Buch Bjerg west: 200 m. west of 71° 31.31′N , 22° 42.41′W; WWA coll. 7/20/01,
Field no. G01/sample 3
Tait Bjerg: 71° 28.421′N , 22° 38.893′W; WWA & party coll. 7/29/01,
Field no. G01/sample 4

DINOSAUR FOOTPRINTS FROM THE "RACEWAY" LOCALITY ON WOOD BJERG

(71° 24.88'N, 22° 33.17'W)

4 blocks

DINOSAUR FOOTPRINTS FROM VARIOUS LOCALITIES ON TAIT BJERG

(vicinity of 71° 28.649′N, 22° 38.920′W)

20 blocks