A review of Palaeozoic and Mesozoic tetrapods from Greenland

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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.

Keywords: Greenland, tetrapoda, marine reptiles, archosauria, trace fossils.

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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 discoveries in Greenland are recorded from the Devonian of Ymer Ø (East Greenland, Fig. 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. 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. 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 tes-

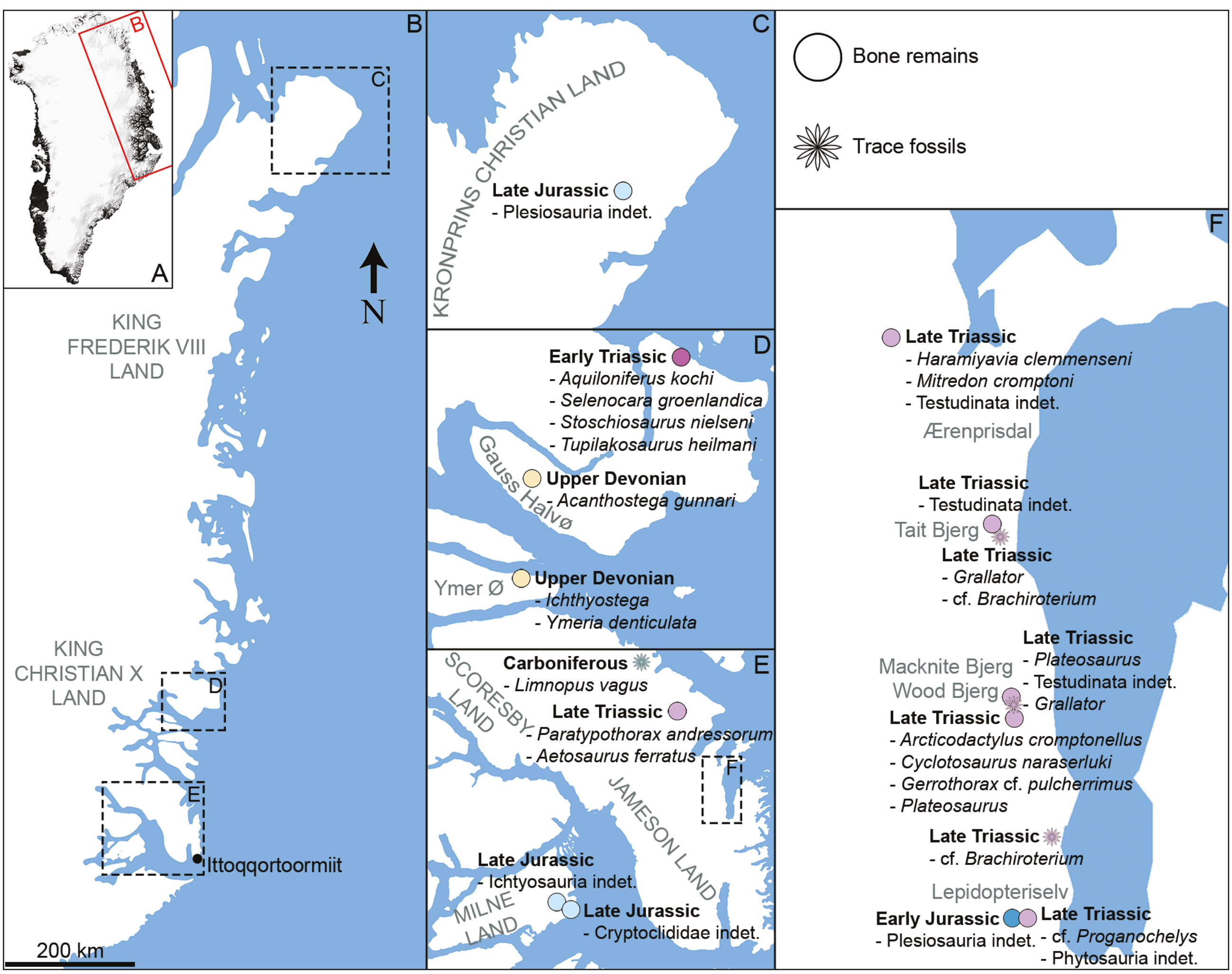

Fig. 1. A–F: Maps showing the position of the main fossil tetrapod sites of Greenland.

tudinatans, 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. 1D), Surlyk *et al*. (2017) for the Wordie Creek Group (Fig. 1D), and Clemmensen (1980b) for the Fleming Fjord Formation (Fig. 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. 1–2). 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. 1C).

Abbreviations. MCZ, Museum of Comparative Zoology, Harvard University (Massachusetts, USA); MGUH, Geological Museum, Copenhagen, Denmark; NHMD, Natural History Museum of Denmark, Copenhagen.

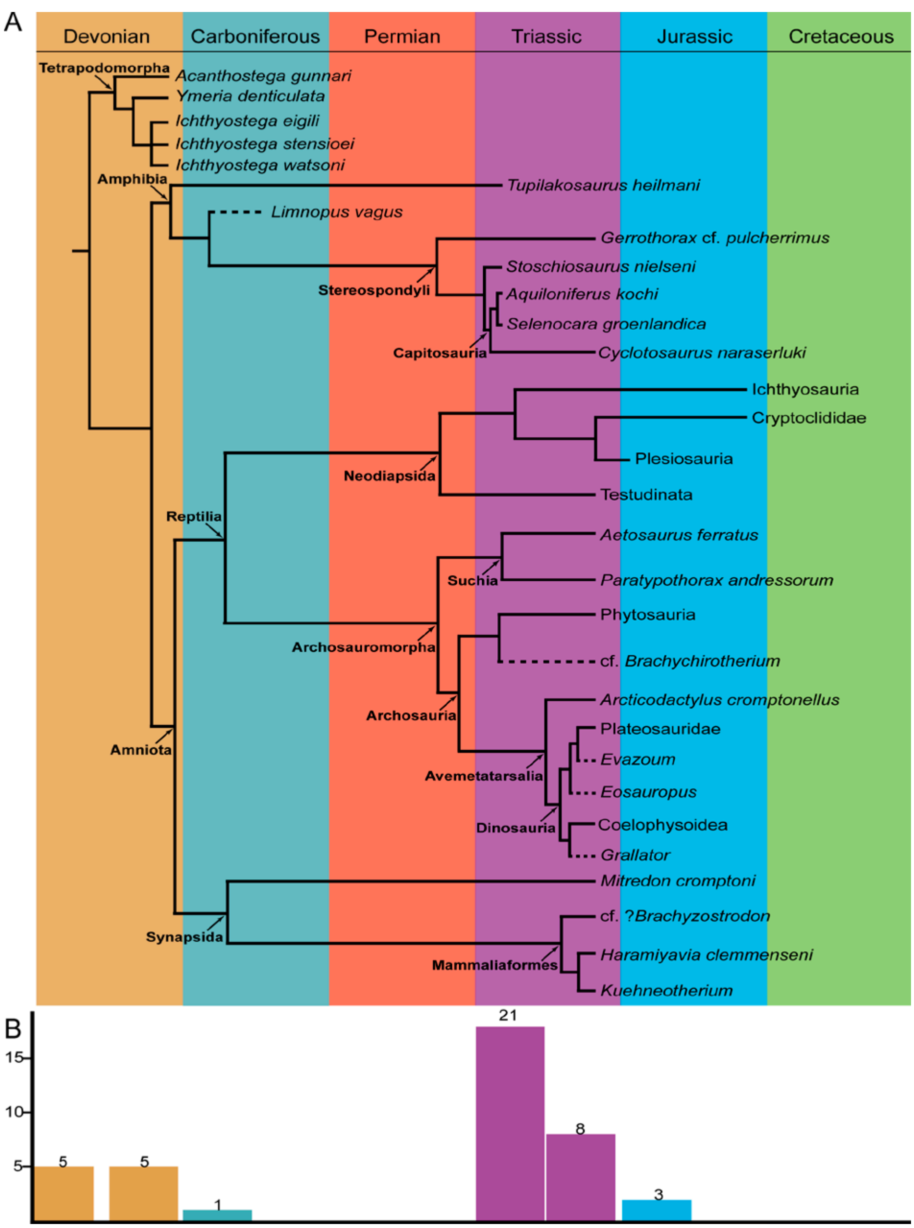

Fig. 2. Main fossil tetrapod taxa of Greenland. **A**: Time calibrated phylogenetic cladogram with major nodes enlightened with arrows and bold headings (for major clades relationships see Ruta *et al*. 2007; Schoch 2008; Brusatte *et al*. 2011; Clack *et al*. 2012; Benton 2014). Dashed lines stand for 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.

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).

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. 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-

Fig. 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.

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. 3).

Localities. Wiman Bjerg & Stensiö Bjerg, Gauss Halvø (Fig. 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. 4); *I. stensioi* Säve-Söderbergh 1932 - MGUH VP 6001, a partial skull with skull roof and anterior palate (Fig. 5); *I. watsoni* Säve-Söderbergh 1932 - MGUH VP 6003, an almost complete skull (Fig. 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).

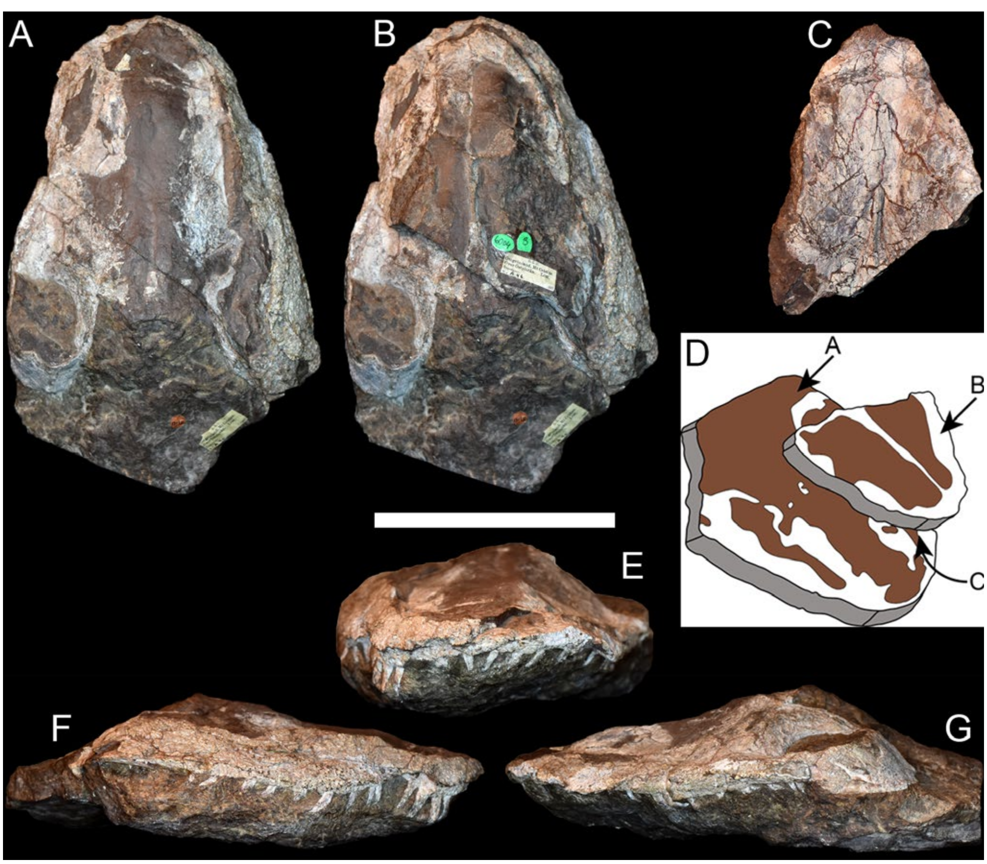

Fig. 4. The stem tetrapod *Ichthyostega eigili* Säve-Söderbergh 1932, holotype MGUH VP 6004 from Late Devonian of the Aina Dal and Britta Dal Formations. **A**–**B**: Dorsal views **C**: Ventral view. **D**: Schematic drawing of MGUH VP 6004 with correspondent views of A, B, and C, out of scale and with exaggerated thickness. **E**: Frontal view. **F**: Right lateral view. **G**: Left lateral view. Scale bar A–C, E–G: 10 cm.

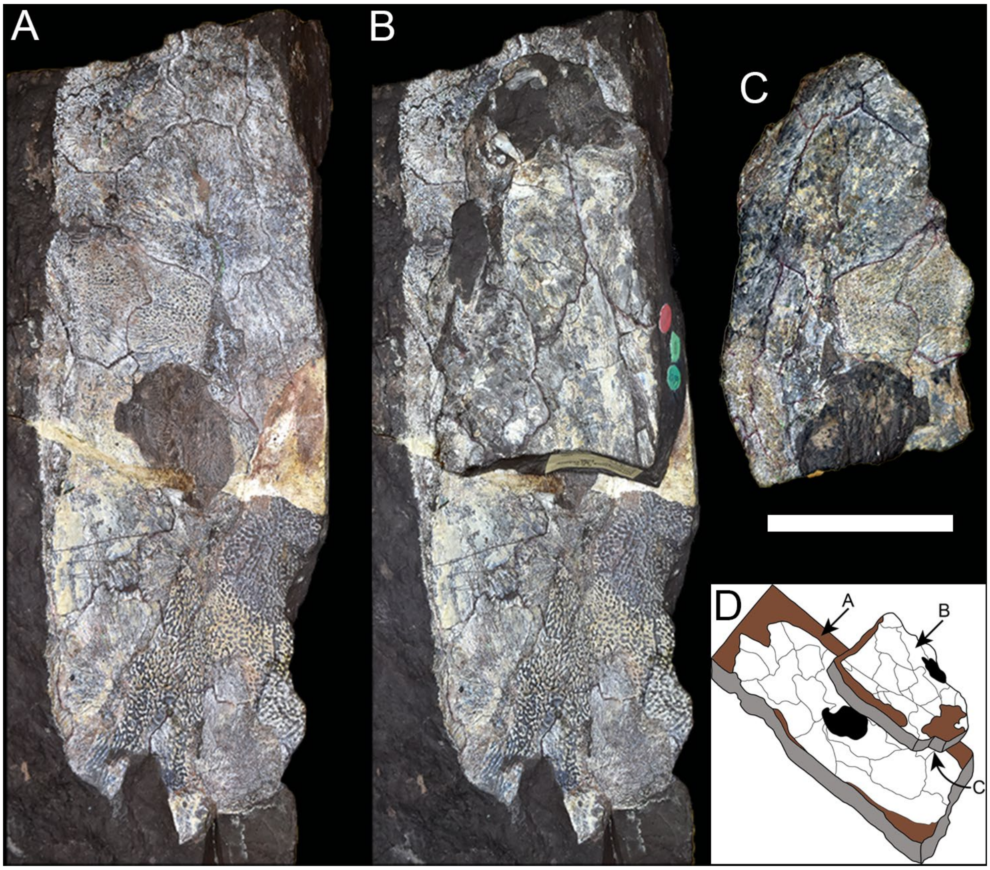

Fig. 5. The stem tetrapod *Ichthyostega stensioi* Säve-Söderbergh 1932, holotype MGUH VP 6001: partial skull from Late Devonian of the Aina Dal and Britta Dal Formations. **A**–**B**: Dorsal views. **C**: Ventral view. **D**: Schematic drawing of MGUH VP 6001 with correspondent views of A, B, and C,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

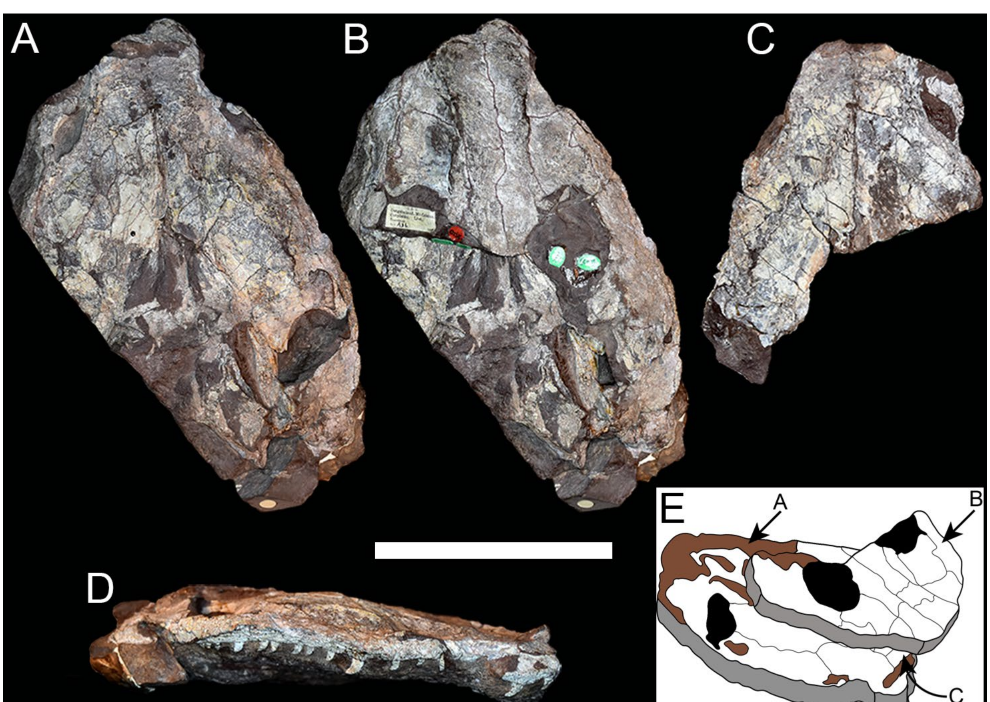

Fig. 6. The stem tetrapod *Ichthyostega watsoni* Säve-Söderbergh 1932, holotype MGUH VP 6003: partial skull from Late Devonian of the Aina Dal and Britta Dal Formations. **A**–**B**: Dorsal views. **C**: Ventral view. **D**: Right lateral view. **E**: Schematic drawing of MGUH VP 6001 with correspondent views of A, B, and C, out of scale and with exaggerated thickness. Scale bar A–D: 10 cm.

***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. 7).

Locality. South side of Celsius Bjerg, Ymer Ø (Fig. 1D).

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

Age. Late Devonian (Famennian).

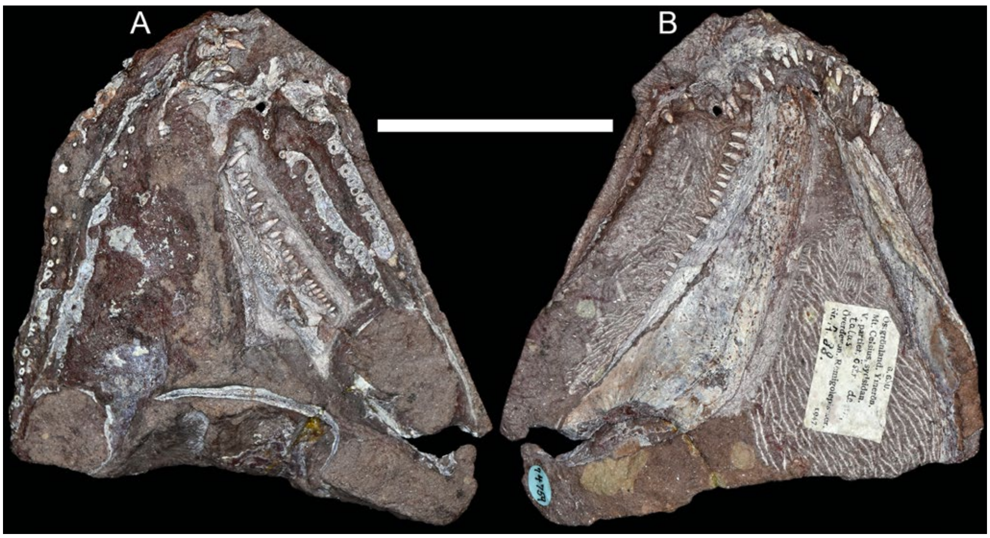

Fig 7. The stem tetrapod *Ymeria denticulata* Clack *et al*. 2012, holotype NHMD 74759 (previously MGUH VP 6088), a partial skull with lower jaws from Late Devonian of the Britta Dal Formation. **A**: Dorsal view. **B**: Ventral view. Scale bar: 5 cm.

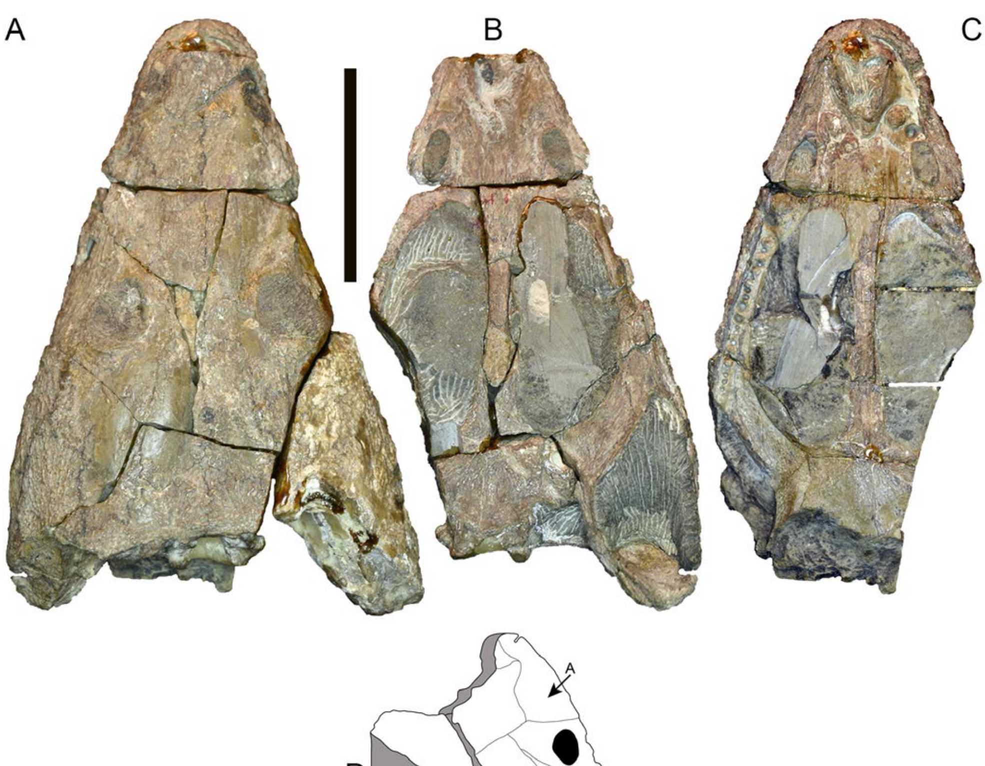

Fig. 8. The capitosauroid *Aquiloniferus kochi* Bjerring 1999, holotype MGUH VP 3357 (previously MGUH VP At.1): a skull from the Early Triassic of the Wordie Creek Group. **A**, **C**: Dorsal views. **B**: Ventral view. **D**: Schematic drawing of MGUH VP 3357 with correspondent views of A, B, and C (out of scale and with exaggerated thickness). Scale bar A–C: 5 cm.

Carboniferous

Trace fossil

***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. 1E).

Horizon. Non-marine dark brown, fine- to medium-grained 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.

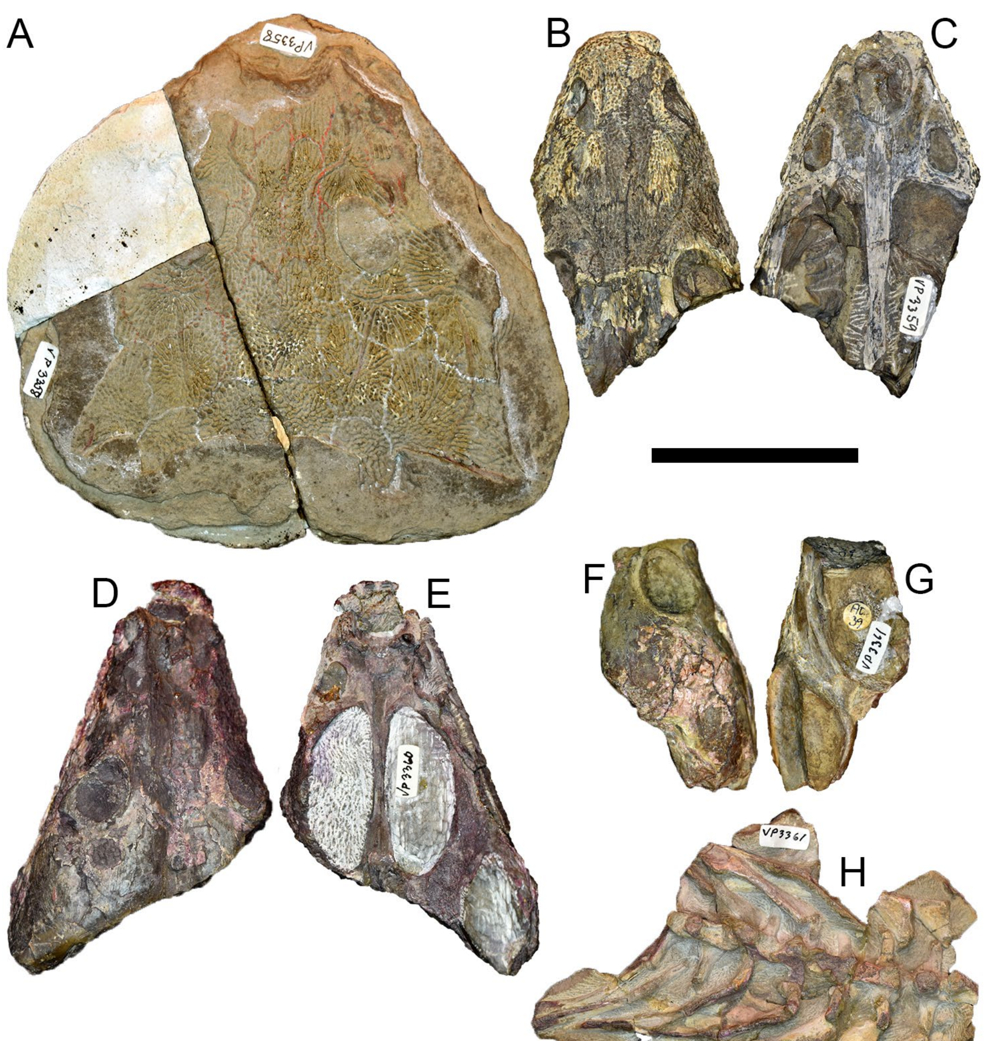

Fig. 9. The capitosauroid *Aquiloniferus kochi* Bjerring 1999: specimens from the Early Triassic of the Wordie Creek Group. **A**: Dorsal view of MGUH VP 3358 (previously MGUH VP At. 3), natural internal cast of a partial skull. **B**–**C**: Dorsal and ventral views of MGUH 3359 (previously MGUH VP At. 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.

Triassic

Skeletal fossils

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

Holotype. MGUH VP 3357 (previously MGUH VP At.1), a skull (Fig. 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. 9).

Locality. South-east of Kap Stosch, Stensiö Plateau and Spath 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. Cosgriff (1984); Lucas (1998); Bjerring (1999).

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

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

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

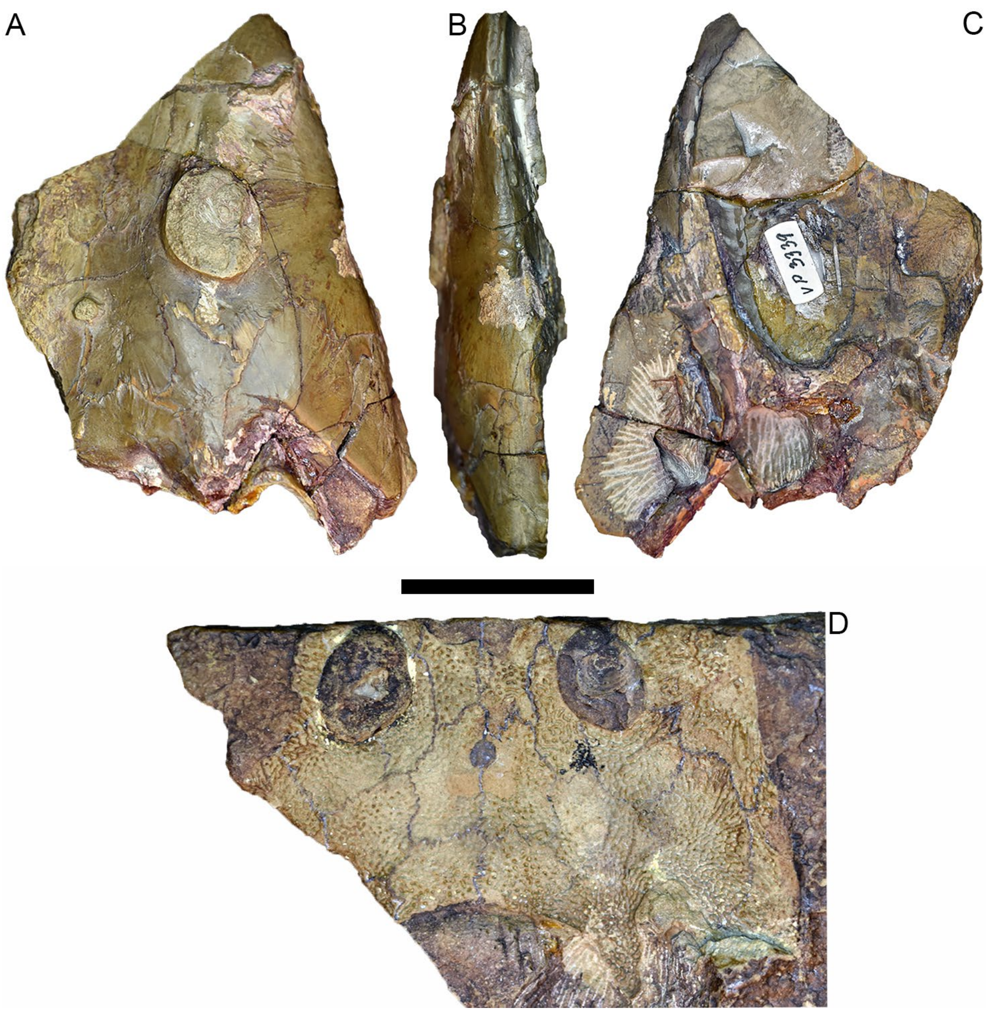

Fig. 10. The capitosaurid *Selenocara groenlandica* Bjerring 1997, holotype MGUH VP 3339 (previously MGUH VP At. 2): a partial skull from the Early Triassic of the Wordie Creek Group, in **A:** Dorsal views, **B**: Lateral right view, and **C**: Ventral views; and natural cast of partial skull MGUH VP 3340 (previously MGUH VP At. 17) (D), from the Early Triassic of the Wordie Creek Group in **D:** dorsal view. Scale bar: 3 cm.

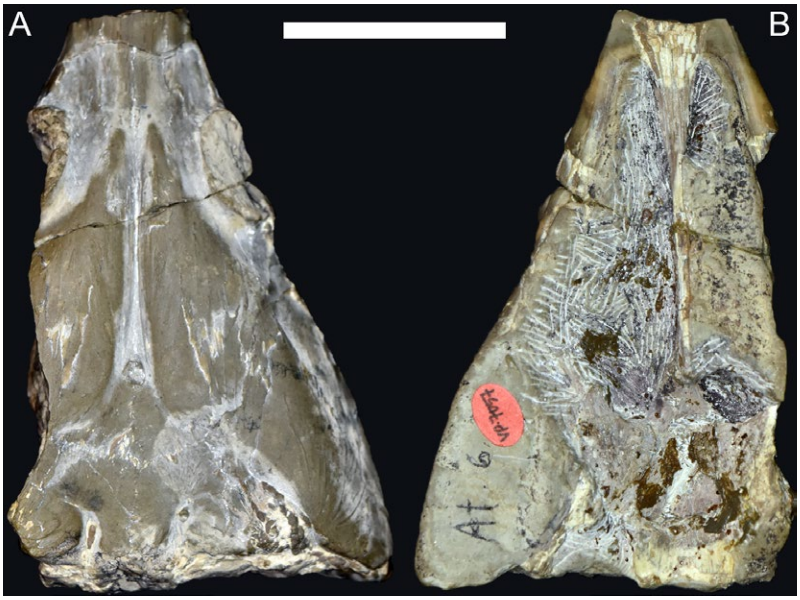

Fig. 11. The trematosaurid *Stoschiosaurus nielseni* Säve-Söderbergh 1935, holotpye MGUH VP 7057 (previously MGUH VP At.6): a partial skull. **A**: Dorsal view. **B**: Ventral view. Scale bar: 3 cm.

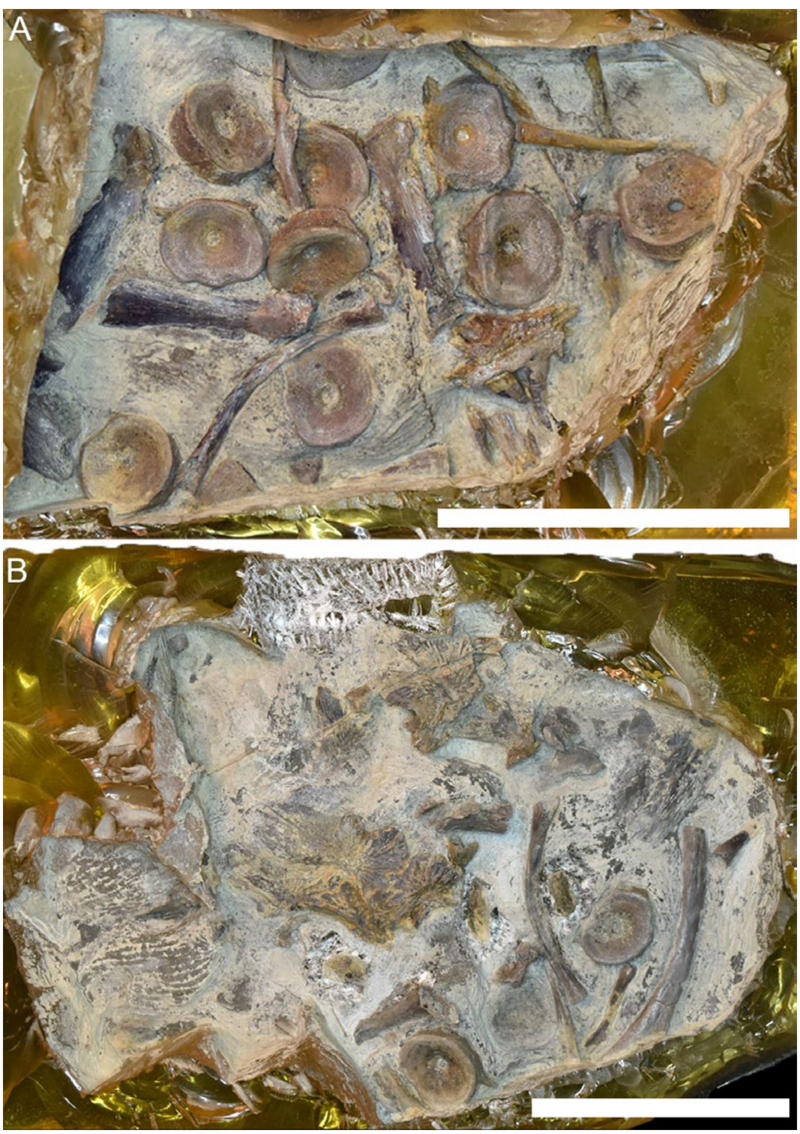

Fig. 12. The tupilakosaurid *Tupilakosaurus heilmani* Nielsen 1954, holotype MGUH VP 3328 (specimen A): two separate blocks containing postcranial material (including vertebrae, ribs, tooth) from the Early Triassic of the Wordie Creek Group. **A**: Block A. **B**: Block B. Scale bars: 5 cm.

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. 11).

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, 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. 12).

Locality. South-east of Kap Stosch, 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. Nielsen (1954, 1967).

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

Holotype. MGUH.VP 9522, a nearly complete skull (Fig. 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. 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. 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. 13C).

Locality. Lepidopteriselv, Jameson Land, 71°15.760′ N, 22°32.682′ W, 285 m a.s.l. (Fig. 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. 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. 13B).

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

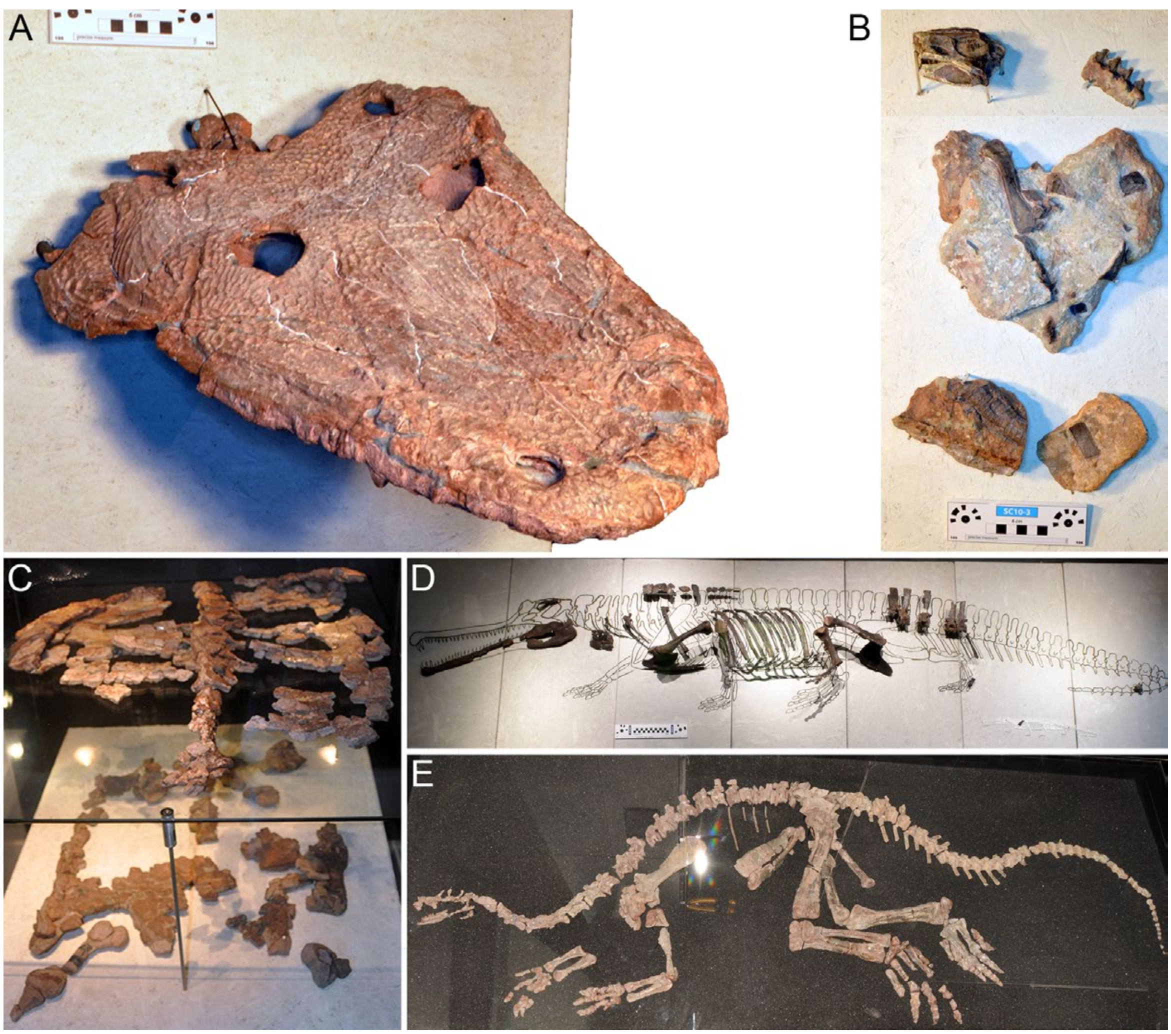

Fig. 13. Fossil tetrapods from the Late Triassic of Jameson Land Basin in exhibition at the GeoCenter of Møns Klint, Denmark, as of 2016. **A**: Oblique photograph of the holotype of the capitosaurid *Cyclotosaurus naraserluki* Marzola *et al*. 2017b MGUH.VP 9522. **B**: The stagonolepidid *Aetosaurus ferratus* Fraas 1877 NHMD 190375–190379 (previously MCZ Field no. 22/92G). **C**: Oblique photograph of the testudine 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.

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.

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. 13D).

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

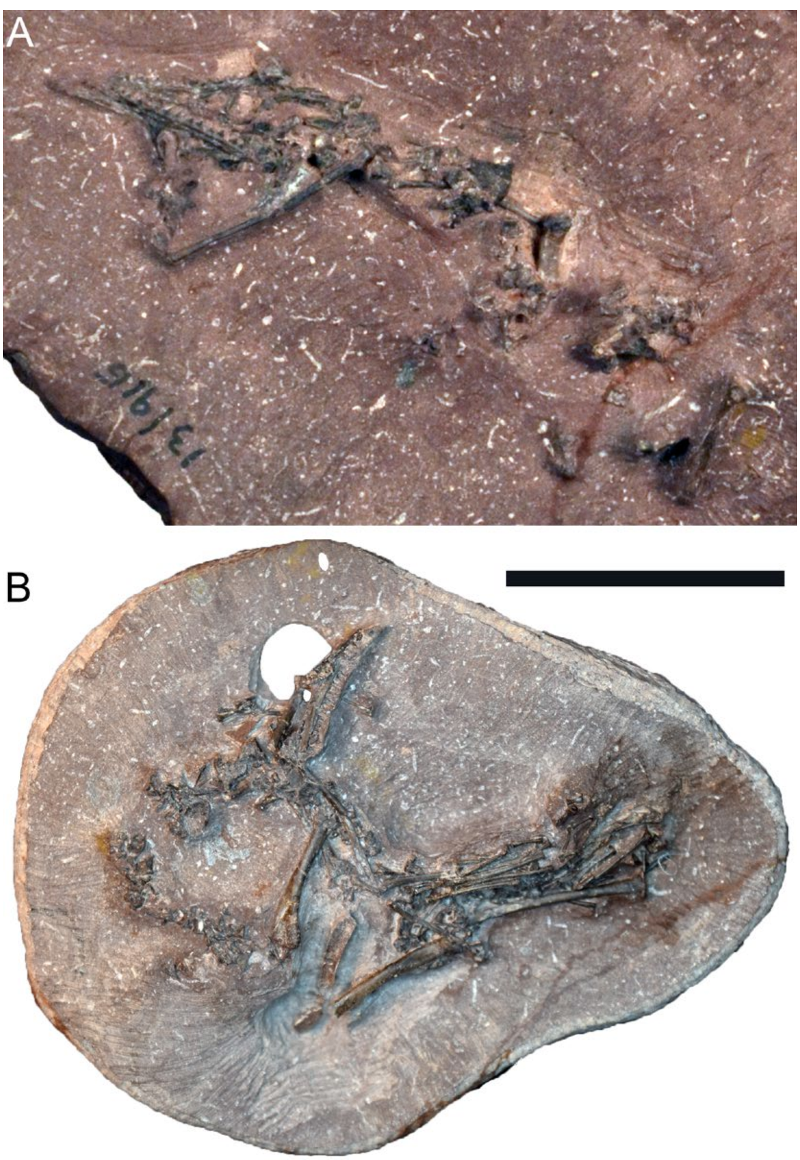

Fig. 14. The eudimorphodontid *Arcticodactylus cromptonellus* (Jenkins *et al*. 2001), holotype NHMD 74799 from the Late Triassic of the Fleming Fjord Formation. **A**: block exposed in the GeoCenter (as for 2016). **B**: counter block at NHMD. Scale bar: 3 cm.

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

Holotype. NHMD 74799, a disarticulated skeleton preserving numerous cranial and postcranial elements (Fig. 14).

Locality. Macknight Bjerg, Jameson Land, 71°22.277′ N, 22°33.341′ W (Fig. 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. 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. 1F).

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*.

Fig. 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.

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

Holotype. MGUH VP 3392, an incomplete left mandible with teeth (Fig. 15).

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

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. 16A–B).

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

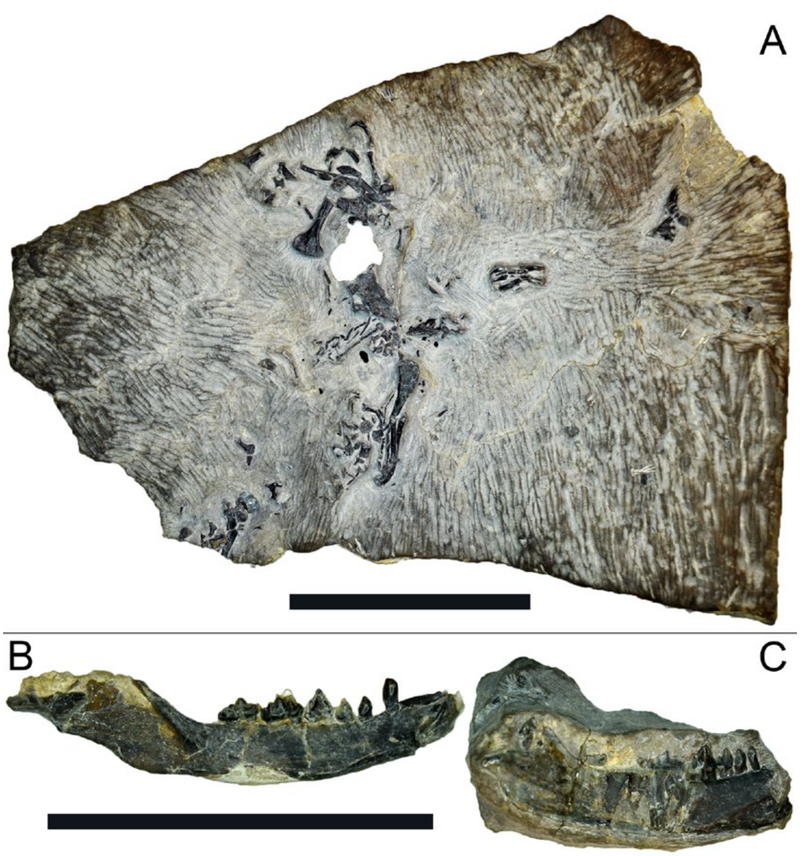

Fig. 16. The haramiyid *Haramiyavia clemmenseni* Jenkins *et al*. 1997, holotype MCZ 7-G95 from the Late Triassic of the Fleming Fjord Formation. **A**: Main block with cranial and postcranial elements. **B**: Right mandible in labial view. **C**: Left mandible in lingual view. Scale bars, A: 5 cm; B and C: 2 cm.

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, 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. 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. 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. 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. 1F).

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. 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. 1F).

Fig. 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.

Fig 18. The cryptoclidid plesiosaur MGUH VP 28378: partial skeleton from the Kimmeridgian (Late Jurassic) of East Milne Land, Scoresby Sund. Scale bar: 20 cm.

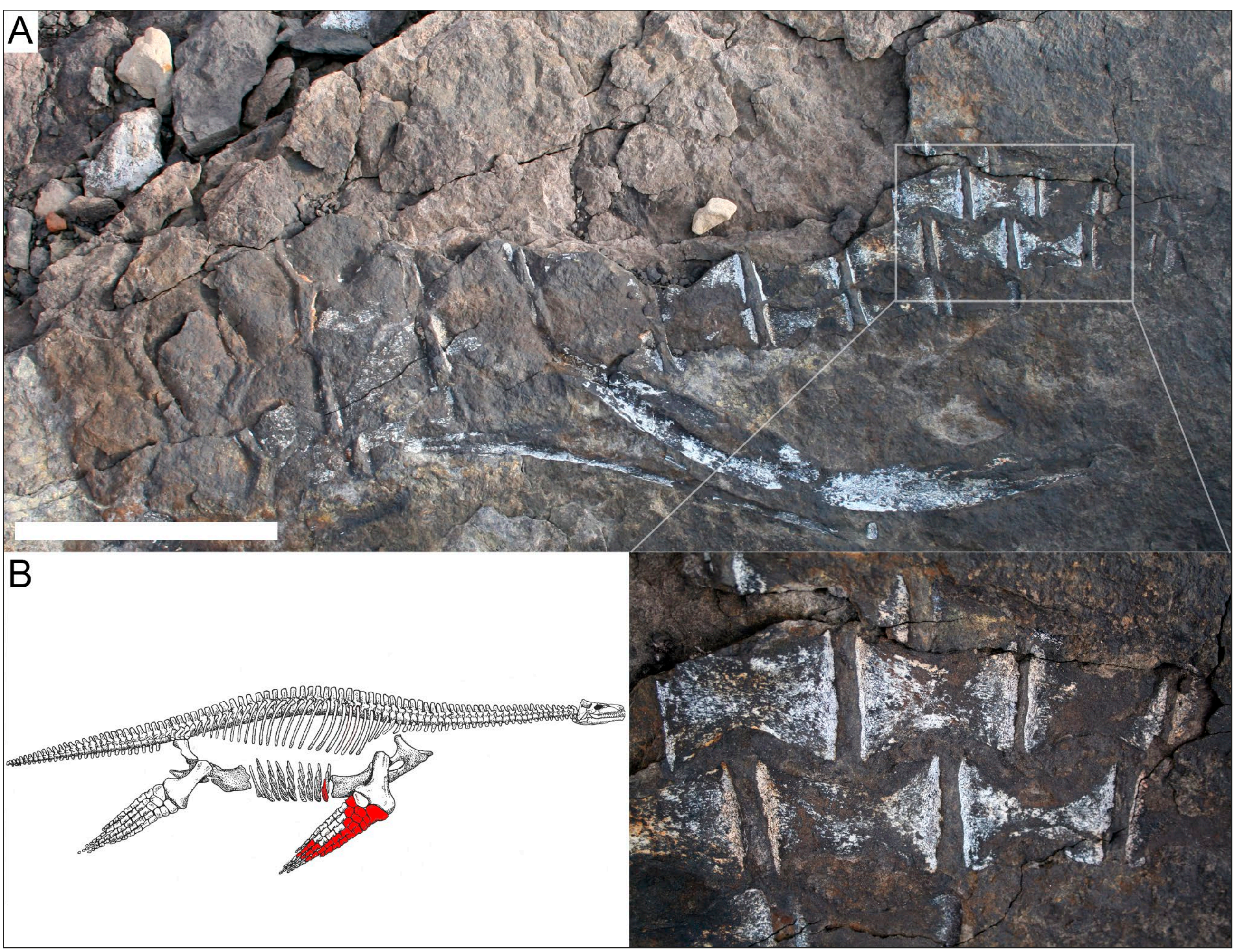

Fig 19. Late Jurassic plesiosaur from Kilen. **A**: The frontal right paddle as found on the field. **B**: reconstruction of the surveyed material using *Cryptoclidus* from Andrews (1910) as model. Scale bar in A: 20 cm.

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. 18).

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

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. 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

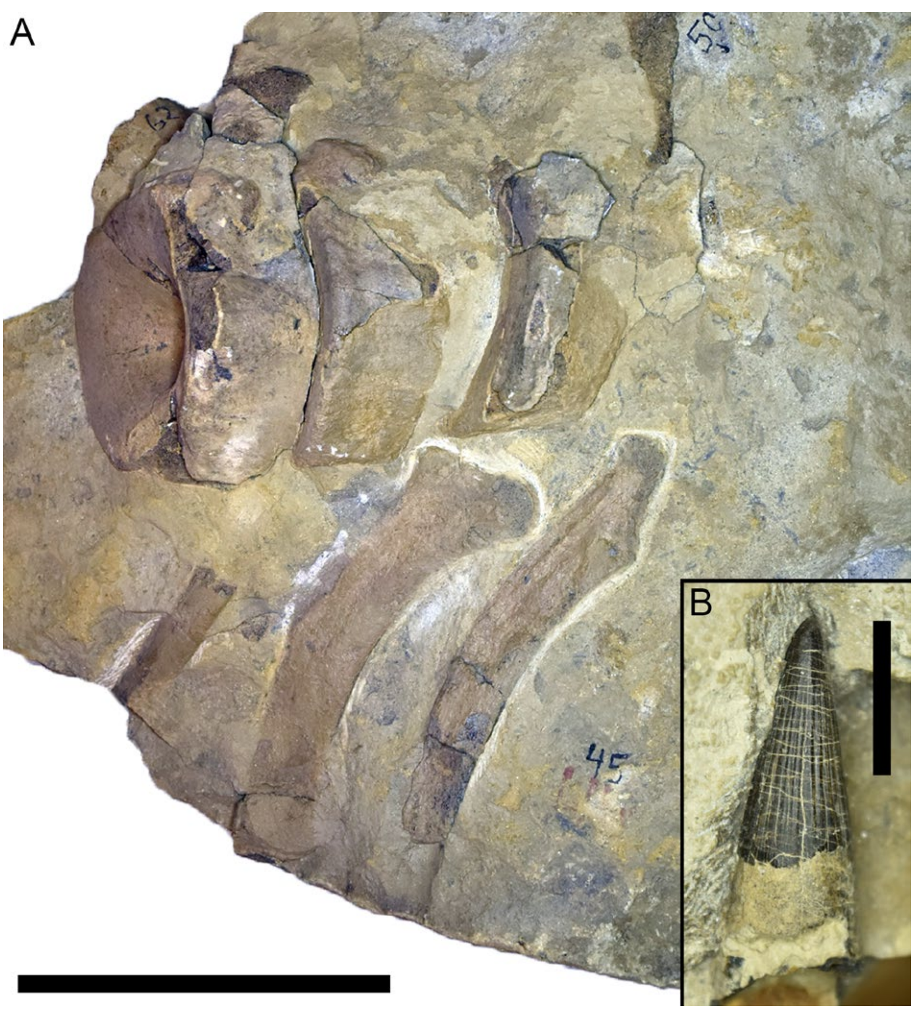

Fig. 20. Undetermined ichthyosaur NHMD 74798 from the Upper Kimmeridgian (Late Jurassic) of the Kap Leslie Formation. in Milne Land, Scoresbysund. **A**: Block including three vertebrae and ribs. **B**: Tooth. Scale bars, A: 10 cm; B: 1 cm.

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. 19).

Ichthyosauria *indet*. (Diapsida: Ichthyopterygia)

Referred specimen: NHMD 74798, includes fragmentary blocks that preserve three vertebrae with ribs and a tooth (Fig. 20).

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

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